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Contrasting abundance and residency patterns of two sympatric populations of transient killer whales (*Orcinus orca*) in the northern Gulf of Alaska

Craig O. Matkin (contact author)[1]
John W. Durban[2,3]
Eva L. Saulitis[1]
Russel D. Andrews[4]
Janice M. Straley[5]
Dena R. Matkin[1]
Graeme M. Ellis[6]

Email address for contact author: cmatkin@acsalaska.net

[1] North Gulf Oceanic Society
3430 Main St., Suite B1
Homer, AK 99603

[2] National Marine Mammal Laboratory
Alaska Fisheries Science Center
National Marine Fisheries Service, NOAA
7600 Sand Point Way NE
Seattle, WA 98115

[3] Protected Resources Division
Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
3333 N. Torrey Pines Ct.
La Jolla, CA 92037

[4] School of Fisheries and Ocean Sciences
University of Alaska Fairbanks
and Alaska SeaLife Center
301 Railway Ave.
Seward, AK 99664

[5] University of Alaska Southeast
Sitka Campus
1332 Seward Ave.
Sitka, AK 99835

[6] Department of Fisheries and Oceans
Pacific Biological Station
3190 Hammond Bay Rd.
Nanaimo, British Columbia, V9R 5K6 Canada

Abstract—Two sympatric populations of "transient" (mammal-eating) killer whales were photo-identified over 27 years (1984–2010) in Prince William Sound and Kenai Fjords, coastal waters of the northern Gulf of Alaska (GOA). A total of 88 individuals were identified during 203 encounters with "AT1" transients (22 individuals) and 91 encounters with "GOA" transients (66 individuals). The median number of individuals identified annually was similar for both populations (AT1=7; GOA=8), but mark-recapture estimates showed the AT1 whales to have much higher fidelity to the study area, whereas the GOA whales had a higher exchange of individuals. Apparent survival estimates were generally high for both populations, but there was a significant reduction in the survival of AT1 transients after the *Exxon Valdez* oil spill in 1989, with an abrupt decline in estimated abundance from a high of 22 in 1989 to a low of seven whales at the end of 2010. There was no detectable decline in GOA population abundance or survival over the same period, but abundance ranged from just 6 to 18 whales annually. Resighting data from adjacent coastal waters and movement tracks from satellite tags further indicated that the GOA whales are part of a larger population with a more extensive range, whereas AT1 whales are resident to the study area.

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Killer whales (*Orcinus orca*) in the eastern North Pacific can be genetically and acoustically separated into three nonassociating lineages: "resident," "transient," and "offshore" (Ford and Ellis, 1999; Matkin et al., 1999; Barrett-Lennard, 2000; Yurk et al., 2002). Of these lineages, Morin et al. (2010) found the transients to be the most genetically divergent and indicated that they should be considered a separate species. Only the transient form has been observed consuming marine mammals in this region and observations indicate that they feed on marine mammals exclusively (Ford et al., 1998; Saulitis et al., 2000; Herman et al., 2005; Matkin et al., 2007a, 2007b; Barrett-Lennard et al., 2011). The potential for these whales to affect trajectories of prey populations has led to considerable debate over the role of predation by transient killer whales in the decline of coastal pinnipeds and sea otters in western Alaska (e.g., Estes et al., 1998, 2009; Springer et al., 2003, 2008; DeMaster et al., 2006; Wade et al., 2007, 2009). In addition to data on feeding habits, evaluation of their top-down impact requires data on abundance and residency patterns of these transient killer whales within specific marine systems, particularly with respect to the abundance and trends of their primary prey.

The coastal waters of Prince William Sound and the Kenai Fjords in the northern Gulf of Alaska are unique in being regularly used by two sympatric populations of transient killer whales (Matkin et al., 1999). Members of both the Gulf of Alaska-Aleutian Islands–Bering Sea transient stock and the AT1 transient stock (Allen and Angliss, 2010) have been photographically identified over the past 27 summer seasons (Matkin et al., 1999, 2008). Individuals from both populations regularly use the same region but have never been recorded swimming together and do not associate (Matkin et al., 1999), and they can be separated by behavior (Matkin et al., 1999; Saulitis et al., 2000), by acoustics (Yurk et al., 2002, 2010; Saulitis

et al., 2005), and by genetics (Barrett-Lennard et al., 2000).

Because of the lack of conclusive studies of genetic divergence across their range, the Gulf of Alaska–Aleutian Islands–Bering Sea transient stock includes all transient killer whales found in Alaskan waters west of southeastern Alaska other than the AT1 stock (Allen and Angliss, 2010). However, photographic mark-recapture analyses indicate little apparent overlap between the Gulf of Alaska whales and the western segment of the stock (Matkin et al., 2007a; Durban et al., 2010). In this article we will refer to the non-AT1 transients in the study area only as the Gulf of Alaska (GOA) transient population and consider their range to be the Gulf of Alaska and north gulf coast, which stretches from southeastern Alaska west through the Kodiak Island region. Although the full range and offshore distribution of the GOA transients is poorly defined, they have been photographed irregularly to the southwest of Prince William Sound–Kenai Fjords study area in Kachemak Bay, lower Cook Inlet, and Kodiak Island waters (Maniscalco et al., 2007; Matkin et al., 1999; C. Matkin, unpubl. data).

The AT1 transients are considered a separate stock, are classified as depleted under the Marine Mammal Protection Act, and currently number only seven individuals (Allen and Angliss, 2010). The home range of the AT1 transient population appears much more restricted than that of the sympatric GOA transients (Matkin et al., 1999; Scheel et al., 2001) or the parapatric west coast transients of southeastern Alaska, British Columbia, and Washington State coastal waters (Ford and Ellis, 1999). AT1 individuals have not been identified outside of the coastal waters of Prince William Sound and the Kenai Fjords (Matkin et al., 1999; Saulitis et al., 2005). Because of its limited range, small population size, and the consistent resightings of subgroups and individuals, the population dynamics of the AT1 population have been monitored directly from annual photographic data (Matkin et al., 2008). However, for the GOA transients, the infrequent resightings of individuals, fluidity in group structure, and larger population size have made it impossible to directly track births and deaths and require a mark-recapture sampling approach to estimate abundance and assess population changes.

In this article we fit mark-recapture models to long-term photographic identification data (1984 to 2010) to examine abundance trends, site fidelity, and demography for the AT1 and GOA transients in the coastal waters of Prince William Sound and the Kenai Fjords. We compare our results with previously described changes in the AT1 population (Matkin et al., 2008) and contrast these results with our parallel analysis of the GOA transient population. We use photographic resighting data and satellite telemetry data to further differentiate the range of the two populations and provide a context for their differing abundance trends.

Materials and methods

Photographic mark-recapture

Identification photographs of killer whales were obtained from the waters of Prince William Sound, Kenai Fjords National Park, and the adjacent coastal waters of the northern Gulf of Alaska (Fig. 1A). The entire region was not surveyed in any given year; however, survey effort was focused towards Prince William Sound in the earlier years of the study (1980s) and was more evenly balanced across the region in later years. Photographic surveys were conducted between April and September over the 27-year period between 1984 and 2010. In order to increase capture probabilities, survey effort was focused in areas known to be used by killer whales, or in response to sighting reports. Data were collected from a variety of platforms; all were small vessels less than 15 meters in length powered by either gasoline-outboard or diesel-inboard engines.

During an encounter, whales were approached at a distance of 15 to 45 m and photographs were taken of the left side of each whale present, showing details of the dorsal fin and saddle patch (Matkin et al., 1999). Photographs were obtained with either 1) a Nikon F-100 SLR camera[1] with fixed 300-mm lens and Fuji Neopan 1600 black and white film, or 2) Nikon D70 and D200 digital cameras with 80–200 mm zoom or 300-mm fixed lenses. Individual whales were distinguished by the shape and pattern of natural markings on their dorsal fins and adjacent saddle patch (Matkin et al., 1999) and were subsequently matched to catalogs of photographs from previous years. Individual matches were corroborated by using co-occurrence with consistent associates because transient killer whales have been shown to travel in stable (and often life-long) matrilineal groupings (Ford and Ellis 1999; Matkin et al., 1999). Photographs were evaluated for quality, and only photographs resulting in reliable identifications were used. Typically, the entire group was photographed. Membership in the AT1 or GOA transient population was determined either by genetic sampling, acoustic analysis, or observation of repeated association with other members of the population.

We treated these photographic identifications and re-identifications as "captures" and "recaptures" to which analytical mark-recapture techniques could be applied for estimation of abundance and demographic parameters (Hammond, 1986, 1987, 1990).

Individual whales were not seen in every year that they were known to be alive, likely in part because of the movement patterns of whales relative to the geographical boundaries of the study area. This factor highlighted the need to allow for temporary emigration in the capture-recapture modeling. The popular Cormack Jolly Seber (CJS) model for estimating survival

[1] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

(Lebreton et al., 1992) does not account for animals that emigrate from the study area and return later. Instead, we followed Whitehead (1990) in developing a mark-recapture model that parameterized emigration and re-immigration probabilities in addition to survival. Our model was based on an individual-specific factorization (e.g., Schofield et al., 2009), allowing modularization into conditional distributions for capture probability, availability of whales for capture (temporary emigration), and death. This formulation allowed imputation of partially observed data on availability in the study area (available in the study area when actually identified) and survival status (alive when identified and between years of repeat identification), providing identifiability of parameters and enabling time-varying formulations. Specifically, the model had the parameters ϕ_t, κ_t, λ_t, and ϖ_t, where ϕ_{t-1} is the probability of survival from time t–1 to time t; λ_{t-1} is the probability of temporary emigration from the study area at time t–1; κ_t is the annual probability of re-immigration back into the study area; and ϖ_t is the probability of capture at time t for whales alive and available to be captured in the study area. Note that owing to the geographic restrictions of the surveys and the likely wider ranging patterns of the whales, survival in this case represented apparent survival that could comprise either death or permanent emigration (at least for the duration of the study).

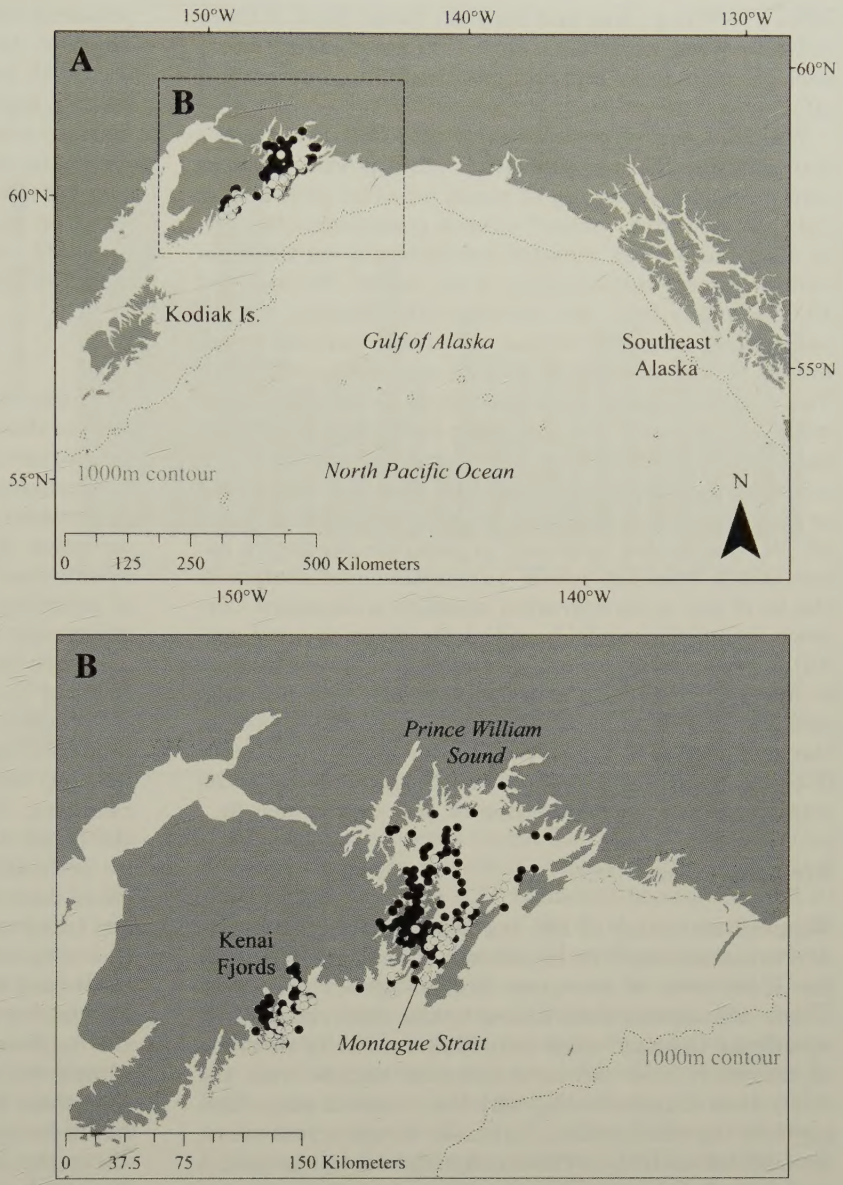

Figure 1

(**A**) Location of the coastal study area of Prince William Sound and Kenai Fjords. (**B**) Locations of encounters with AT1 (203, closed circles) and Gulf of Alaska (GOA) (91, open circles) transient killer whales (*Orcinus orca*) between 1984 and 2010, during which photo-identification data were collected.

To fully quantify uncertainty about the unknown parameters, we adopted a Bayesian approach to model fitting and inference, where estimates were presented as full probability distributions (Gelman et al., 1995). The Bayesian approach requires prior distributions to be specified for all model parameters, and we adopted similar hierarchical priors for each set of probability terms ϕ, λ, κ, and ϖ. To allow temporal variation across each parameter vector, each annual probability was initially specified as a function of a mean for each parameter vector and annual random effects terms:

$$\begin{aligned} \text{logit}(\phi_t, \lambda_t, \kappa_t, \text{and } \varpi_t) &= \text{logit}(\mu^{\phi,\lambda,\kappa,\varpi}) + g^{\phi,\lambda,\kappa,\varpi}\,\varepsilon_t^{\phi,\lambda,\kappa,\varpi} \\ \varepsilon_t^{\phi,\lambda,\kappa,\varpi} &\sim \text{N}(0, \sigma^{\phi,\lambda,\kappa,\varpi}) \\ g^{\phi,\lambda,\kappa,\varpi} &\sim \text{Bernoulli}(0.5), \end{aligned} \quad (1)$$

where $\text{logit}(a) = \log(a/(1-a))$.

The prior distribution for each parameter was thus determined by two hyper-parameters: μ represented the mean value across each set of parameters and the standard deviation term σ represented the year-to-year variability over the set, on the logit scale. Uniform(0,1) prior distributions were placed on each of the five mean probabilities $\mu^{\phi,\lambda,\kappa,\varpi}$ and a uniform(0,10) prior distribution was adopted for $\sigma^{\phi,\lambda,\kappa,\varpi}$ to allow annual differences from the logit-transformed means to emerge. The probability (evidence) of temporal variability in each parameter vector was assessed through indicator vari-

ables $g^{\phi,\lambda,\kappa,\varpi}$ (e.g., Kuo and Mallick, 1998). Each of these indicators was assigned a Bernoulli prior distribution, such that the prior probability of including any annual effect was 0.5.

We used the freely available WinBUGS software (Lunn et al., 2000) to implement Markov Chain Monte Carlo (MCMC) sampling to make repeated draws from the "posterior distribution" of each parameter—the prior distribution was updated conditionally on the data and structural relationships of the model. We sampled 10,000 values from the posterior distribution of each parameter, after discarding an initial burn-in determined by the method of Brooks and Gelman (1998). The sampled values were then used to estimate summary statistics for the posterior distributions. MCMC approaches can similarly be used to sample from the posterior distribution of quantities that can be derived as functions of parameters. Notably, we used the same MCMC simulation approach to generate predictive observations from the model parameters and compared the fit of our re-immigration model to a standard Cormack Jolly Seber model based on the mean squared predicted error (MSPE; Gelfand and Ghosh, 1998; Durban et al., 2010). As with other model selection methods, this predictive approach achieves a compromise between the goodness-of-fit and a penalty for model complexity (Gelfand and Ghosh, 1998). As such, the model with the smallest MSPE was estimated to provide the best fit.

Assessing trends

We used estimates of the capture probabilities (ϖ_t) to derive estimates of the abundance of animals (N_t) using the study area in any given annual survey period (t). These parameters were linked to the observed data by specifying the number of individuals actually observed in the study area (n_t) as a binomial sample from the study area abundance (N_t) with the binomial proportion given by the estimated ϖ_t. To assess trends across years, we modeled each N_t as Poisson distributed and adopted a model for the unknown Poisson means (m_t) that governed the form of the variation between years. Specifically, we therefore adopted a flexible change-point model to describe temporal transitions (e.g., Carlin et al., 1992):

$$\begin{aligned} \log(m_t) &= \beta_0 + g^{\beta}\beta_1\delta(t-c) + \varepsilon_t^N \\ \varepsilon_t^N &\sim \mathrm{N}(0, \sigma^N) \\ g^{\beta} &\sim \text{Bernoulli}(0.5). \end{aligned} \quad (2)$$

The parameter β_0 described the general intercept of the model (or level of abundance on the log scale before the change-point), and the function $\delta()$ represented a step function, defined as 1 if its argument was zero or positive and zero otherwise. The parameter β_1 described the magnitude of a step change (on a log scale), at time c (known as a change-point). We assumed the timing of the change-point was unknown and used the data to assess the evidence for a change-point in each of the 27 years. This problem therefore involved estimating the posterior distribution of the unknown temporal change-point (c) to identify when a change-point may have occurred, and with what probability. The model offers a flexible approach for modelling changes in abundance, because uncertainty about the year of the change-point results in uncertainty over how the trend is apportioned over the time series of between-year transitions. Because the step function $\delta()$ was specified on a discrete time period ($t - c$), we placed a discrete uniform prior for c over T=27 years) (e.g., Carlin et al., 1992):

$$c \sim \mathrm{U}(1,T) \quad (3)$$

with discrete prior probability of $1/T$ being placed on each of the 27 years. We assumed that the direction and magnitude of the change was unknown, and we therefore assigned diffuse prior distributions for the hyperparameters β_0 and β_1, each with mean 0 and standard deviation of 10. We assessed the probability of a trend in abundance by estimating the indicator probability g^{β} of including the trend parameter β_1 in the model for the abundance estimates.

Rather than perform this trend analysis independently of the mark-recapture model, we combined these two components into a single Bayesian hierarchical model to propagate uncertainty in estimation of capture probabilities (ϖ_t) into estimates of abundance (N_t) and trend parameters. We did not assume that the N_t fell exactly on the trend line, or had a common variance, but instead we included annual random-effects terms (ε_t^N) that allowed over-dispersion in contrast to a fixed-effects Poisson trend model. A normal random effects distribution was adopted for the $\varepsilon_t^N \sim \mathrm{N}(0, \sigma^N)$, with overdispersion controlled by the standard deviation (σ^N), which was assigned a uniform (0,10) prior distribution. As with the mark-recapture parameters, we used WinBUGS to sample 10,000 values from the marginal posterior distributions for the annual estimates of abundance, N_t. Additionally, interest was focused on making inference about the posterior distributions of the parameters of the trend model, specifically the change-point (c), the rate of change (β_1), and the probability of a trend (g^{β}).

Tracking whale movements

To examine movements of whales relative to our mark-recapture modeling estimates (extent of temporary emigration away from the study area), we compared photographs used in our analysis with those taken during parallel research efforts in southeastern Alaska, British Columbia, and Washington State (e.g., Ford and Ellis, 1999) to identify annual overlap of individuals. Previous analyses had shown no overlap of AT1 or GOA transients with those in the Aleutian Islands (Durban et al., 2010). In addition, we attached satellite transmitter tags to individual GOA and AT1 transient whales to provide fine-scale tracks of daily movements. The tag design was a low impact minimally percutaneous external-electronics transmitter (LIMPET) satellite tag (Andrews et al., 2008). In this tag, the main electronics package, an Argos-linked, location-only SPOT

5 transmitter (Wildlife Computers, Redmond, WA), is housed in an epoxy casing with dimensions of 65×30×22 mm. The tag is held externally on the dorsal fin of the whale by two 4-mm-diameter medical-grade titanium darts that were affixed to the bottom of the tag, for a total mass of 49 g. The darts were designed to penetrate 6.5 cm into the connective tissue in the dorsal fin and remain embedded with a series of backward-facing barbs which acted as anchors for the darts. The LIMPET tags were projected onto the whales by using a crossbow with 150-lb draw weight, and the tag was held on the end of an arrow in a special rubber boot.

This type of satellite tag transmits ultra-high frequency (UHF) radio signals to Argos receivers onboard weather satellites in sun-synchronous polar orbits. To conserve power, transmissions are limited by a submersion sensor to times when the whale is at the surface. Locations were calculated by the Argos system by the method of least squares (http://www.argos-system.org, accessed October 2007), and we determined the plausibility of each location using the Douglas Argos filter, vers. 7.03 (Douglas[2]). We retained locations with high location accuracies (LC2 and LC3), as well as consecutive points separated by less than 3 km. All other locations were removed if the rate of movement between consecutive locations exceeded 25 km/h or the angle formed by the previous and subsequent locations indicated extreme return-movements. The angle of each triad of points and the distance between the shortest leg of the triad was assessed by the filter and compared with the dimensionless rate coefficient (Ratecoef) that was set to 25. Location data were imported into Google Earth (Google, Mountain View, CA) for basic visual inspection and into ArcMap 9.3.1 (ESRI, Redlands, CA) for further analysis. Distance traveled was calculated for each tagged animal, as well as a calculation of oceanic home range developed by subtracting the land area from the total area in the Minimum Convex Polygon, which was the polygon that described the perimeter of all filtered satellite locations received during the period of attachment.

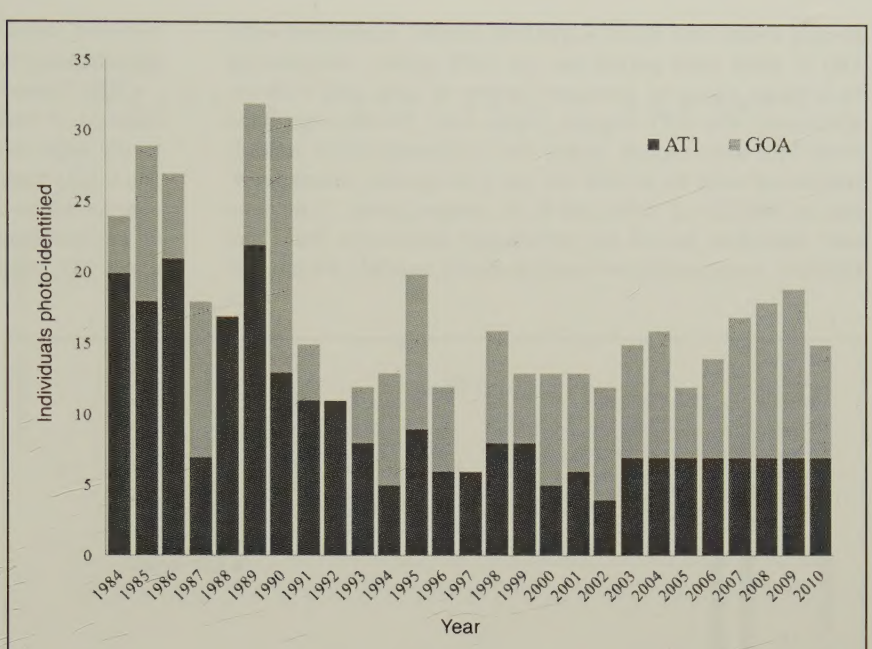

Figure 2

The number of individuals photographically identified from the AT1 and Gulf of Alaska (GOA) transient killer whale (*Orcinus orca*) populations in each annual April–September period, 1984–2010.

Results

During the 27 years of this study we averaged 106 (range=29–249) vessel days per year with at least 59 days logged in all years except for 1987 (29 days). During these surveys we recorded a total of 203 encounters with members of the AT1 transient population and 91 encounters with members of the GOA transient population (Fig. 1). Over 27 annual (May–September) periods, a total of 88 individual whales were documented. There were three times as many GOA individuals (66) as AT1 individuals (22), but the average number of individuals identified in each summer interval was similar for both populations (GOA: median=8, range 0–18; AT1: median=7, range 4–22; Fig. 2). This finding reflected a higher resighting rate for individual AT1 whales; individuals were seen in a median of nine different annual intervals (range 3–25) compared with a median of just two intervals (range 1–16) for GOA whales (Fig. 3). It is notable that 7 of 22 total AT1 whales were identified in more than 20 annual intervals, whereas only 1 of 66 GOA whales was identified in more than 10 intervals (Fig. 3). The number of AT1 individuals seen each year clearly declined across the study period from around 20 individuals in the 1980s to fewer than 10 individuals in the 2000s, whereas the number of GOA individuals remained at a more consistent but low number with a median 8 individuals identified per year (Fig. 2). However, to formally assess changes in abundance, we adjusted our sighting data for capture probabilities using mark-recapture models.

The mark-recapture model with emigration and reimmigration provided a better fit to the photo-identification data than the standard CJS model, for both AT1 and GOA individuals. For GOA whales, there were 49 discrepancies between 1079 observed and predicted data

[2] Douglas, D. 2007. The Douglas Argos-Filter. [Available at http://alaska.usgs.gov/science/biology/spatial/manual.html, accessed 1 October 2007.]

points under the re-immigration model, compared with 190 of 1079 data points for the CJS model, translating to a mean squared predicted error of 0.04 and 0.18 respectively. For AT1 whales, there were 25 discrepancies from 569 data points under the re-immigration model, compared with 91 in 569 for the CJS model, corresponding to MSPEs of 0.04 and 0.16, respectively. Inference was therefore based on parameter estimates from the flexible emigration-re-immigration model, which indicated notable differences in the fidelity of the two populations to the study area (Table 1).

GOA transients showed a much higher rate of exchange of individuals in the study area, with a relatively high probability of emigration (posterior median $\mu^{\lambda}=0.55$) and low rate of re-immigration ($\mu^{\kappa}=0.17$), compared to a low rate of emigration and high rate of re-immigration for the AT1 population ($\mu^{\lambda}=0.08$, $\mu^{\kappa}=0.77$), implying high study area fidelity for the AT1 whales. Similarly, the average probability of capture was higher for AT1($\mu^{\varpi}=0.98$) compared with GOA ($\mu^{\varpi}=0.83$) individuals, implying that almost all of the AT1 individuals in the study area were photographed in each year, likely because of a higher fidelity to the study area and smaller range. Although the average apparent survival was high for both populations (GOA $\mu^{\phi}=0.98$; AT1 $\mu^{\phi}=0.99$), there were noticeable annual deviations from the average (Fig. 4). Although there was a substantial dip in the GOA transients' apparent survival in one year, 1986, there was a consistent trend in the AT1 population, with survival from 1989 to 1990 showing a marked decrease (posterior median=0.68, 95% probability interval=0.48 to 0.86) compared with the overall average, with no overlap in 95% probability intervals between this estimate and those for most other years.

The trends in abundance of the two populations, based on estimates of abundance and parameters of the

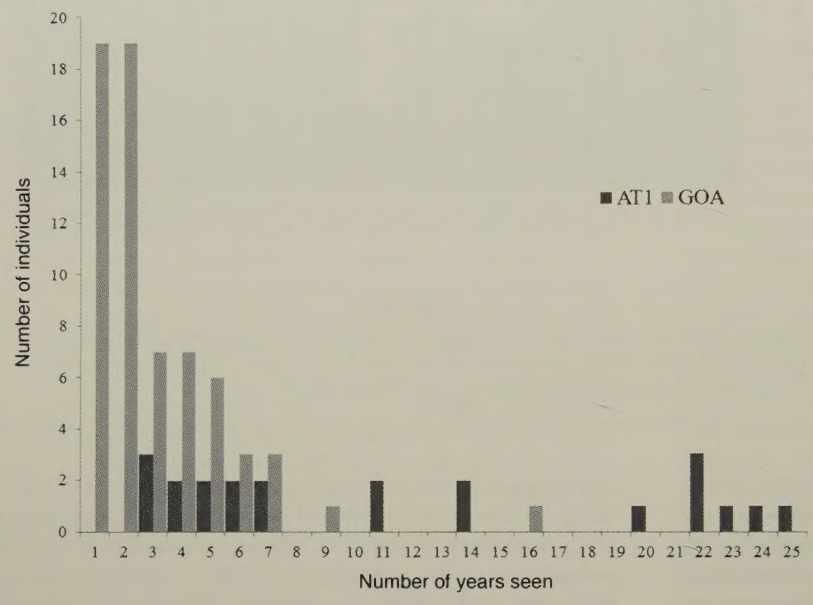

Figure 3

Frequency plot of the number of individual whales photographed in different numbers of annual sampling periods, for both the AT1 and Gulf of Alaska (GOA) transient killer whale (*Orcinus orca*) populations.

Table 1

Fit of photographic identification data to the mark-recapture model with emigration and re-immigration, for both AT1 and Gulf of Alaska (GOA) transient killer whale (*Orcinus orca*) populations. l=the probability that an individual in the study area migrates out of it each year; κ=the probability that an individual not in the study area population migrates back into it each year; ϕ=the annual probability of survival, ϖ=the annual probability of capture (identification) in the study area. Estimates are presented as the 0.025,0.50, and 0.975 probability intervals of the posterior probability distribution (i.e., median surrounded by 95% probability intervals) for the average (μ) value across May–September periods, plus the probability of between-year differences in parameters over the 27 time periods, given by the posterior probability $p(g=1)$ of each respective time-varying indicator variable g. Additionally, the parameter β_1 is included to indicate the magnitude and direction of abundance trend (on the log scale).

	Posterior estimates				
Population	Emigration μ^{λ} [$p(g^{\lambda}=1)$]	Re-immigration μ^{κ} [$p(g^{\kappa}=1)$]	Survival μ^{ϕ} [$p(g^{\phi}=1)$]	Capture μ^{ϖ} [$p(g^{\varpi}=1)$]	Trend β_1 [$p(\beta_1=1)$]
GOA	0.21,0.55,0.80 [1.00]	0.02,0.17,0.67 [1.00]	0.94,0.98,0.99 [1.00]	0.55,0.83,0.99 [1.00]	–1.2,0.1,1.3 [0.02]
AT1	0.02,0.08,0.23 [1.00]	0.18,0.77,0.97 [0.71]	0.96,0.99,1.00 [1.00]	0.92,0.98,1.00 [0.64]	–1.1,–0.8,–0.5 [1.00]

trend model, revealed contrasting patterns (Figs. 5 and 6). The estimated number of GOA whales using the study area in each annual period, N_t, showed relatively little variation from a low posterior median of six whales in 1996 and 2005 to a high of 18 in 1990. The AT1 whales showed evidence of greater abundance changes, from an estimated high of around 22 in 1989 to a low of seven at the end of the series. As a result, there was strong evidence that the abundance of AT1 whales declined over the study period and unequivocal support for inclusion of the trend model for abundance with $p(g^{\beta}=1)=1$. The entire posterior distribution for the trend parameter, β_1, fell below zero, indicating a probability of 1.00 of a downward trend. In contrast, the posterior distribution for the trend parameter was evenly spread above and below zero for GOA whales, with 51% of the posterior density in favor of a negative trend. As a result, there was little support for including a model for trends in abundance with $p(g^{\beta}=1)=0.02$. Correspondingly, the posterior density for the change-point was distributed evenly across all years for GOA whales and reflected no obvious changes in abundance. For AT1 transients, in contrast, there was a distinct peak in the posterior probability distribution for a change-point, and 97% of the posterior density for an abundance change occurred in the five years after 1989.

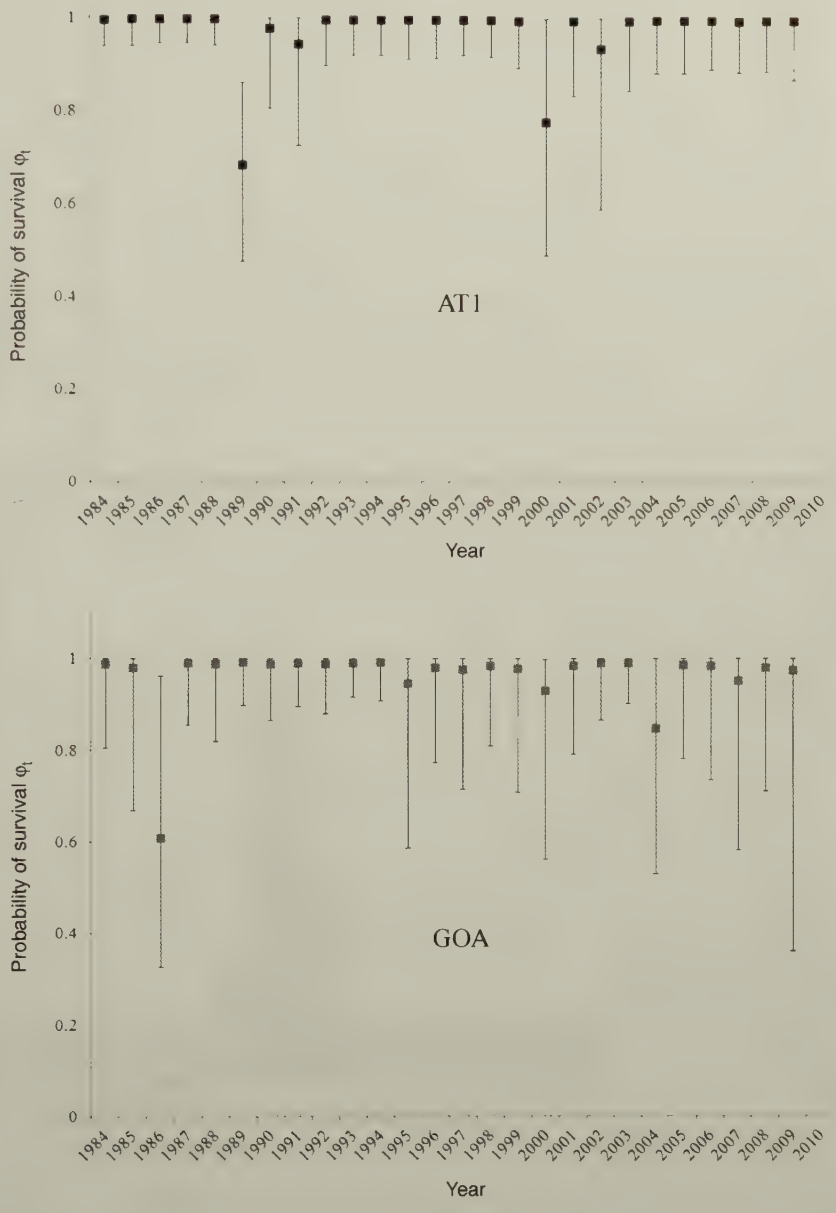

Figure 4

Annual estimates of the probability of survival ϕ_t, for both AT1 and Gulf of Alaska (GOA) transient killer whales (*Orcinus orca*). Solid squares represent the posterior median, and bars represent the 95% probability intervals.

Emigration of GOA transients away from the study area was also supported by photographic resighting data from southeastern Alaska and British Columbia (Table 2). For 1995–2007 there were 16 encounters with GOA transient whales in these adjacent regions, including one (5 June 2001) with GOA transients in association with known members of the west coast transient population (Matkin et al., 2007b). There were no resighting data outside of Prince William Sound–Kenai Fjords for AT1 transients despite substantial survey effort in southeastern Alaska (Dahlheim and White, 2010) and in adjacent regions to the west of the study area (Matkin et al., 1999, 2007a; Durban et al., 2010; senior author, unpubl. data). Additionally, the one tagged AT1 transient did not travel out of the area. All these observations support the inference from the mark-recapture model of high fidelity to the study area.

Satellite-monitored LIMPET tags were attached to GOA transients in Prince William Sound on four occasions for a total of 73 days of transmissions (Table 3). One individual (AT73) was tagged on two occasions in different years. Tagged whales traveled a total distance of 7107 km during 73 days for an average move-

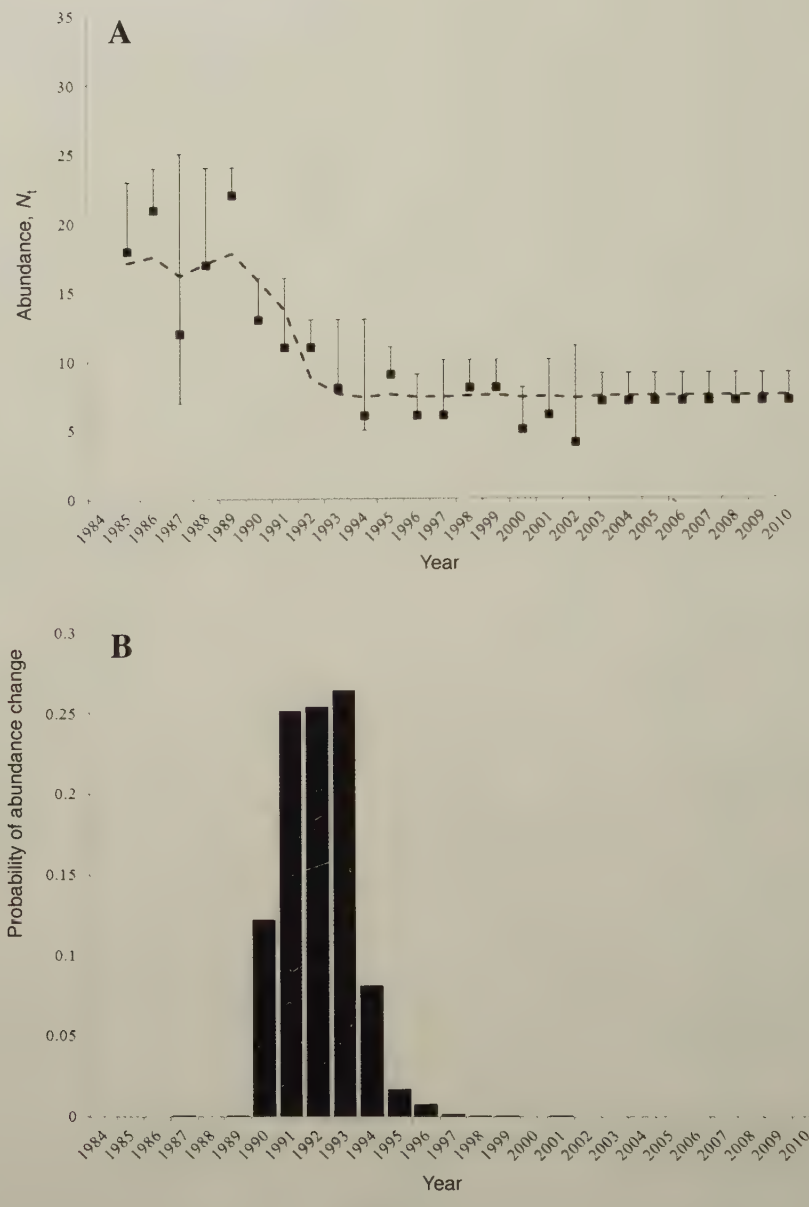

Figure 5

(**A**) Estimates of abundance for AT1 transient killer whales (*Orcinus orca*) in the Prince William Sound–Kenai Fjords study area; solid squares represent the posterior median for the estimated number of whales using the study area in each May–September period, N_t, and bars represent the 95% probability intervals. The broken horizontal line represents the trend given by a change-point model. (**B**) Posterior probability of a change in the abundance level in each year, characterizing the trend model.

ment of 97km/day. Tagged GOA transients traveled as far offshore as 100 km and ranged from northern Kodiak Island to outside waters of southern southeastern Alaska (Fig. 7). The only areas used by the tagged whales in Prince William Sound were ocean entrances and Montague Strait. A single AT1 killer whale was tracked for five days in 2010, and it traveled an average distance of 95km/day. It moved offshore as far as 45 km but did not leave the Kenai Fjords–Prince William Sound area. It was the only tagged whale that traveled up into Prince William Sound, away from the ocean. The pattern of AT1 transients using more inside waters in Prince William Sound and Kenai Fjords, and of GOA transients using ocean entrances, Montague Strait, and the outer coastlines of Kenai Fjords was also reflected in our encounter locations (Fig. 1B).

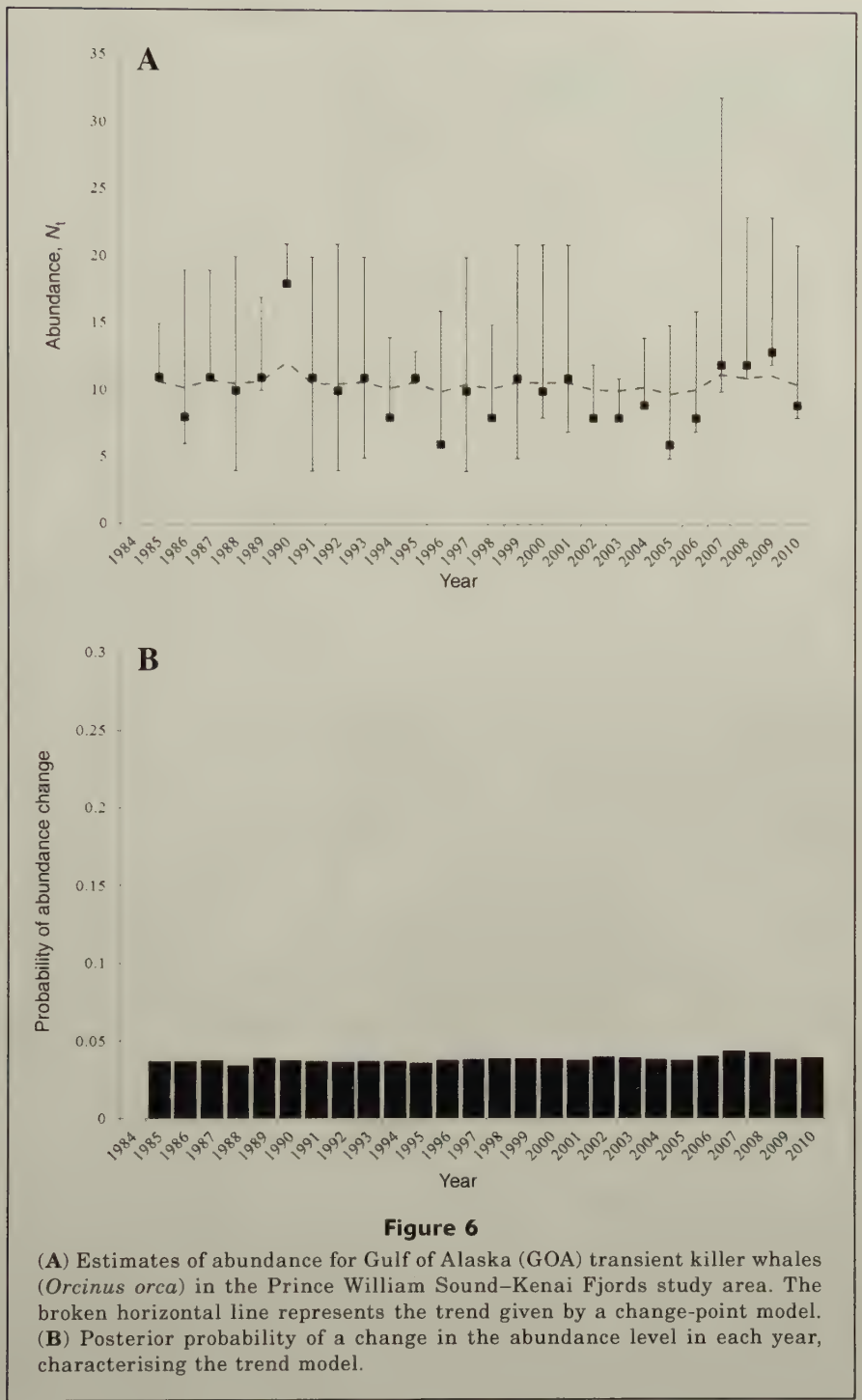

Figure 6

(**A**) Estimates of abundance for Gulf of Alaska (GOA) transient killer whales (*Orcinus orca*) in the Prince William Sound–Kenai Fjords study area. The broken horizontal line represents the trend given by a change-point model. (**B**) Posterior probability of a change in the abundance level in each year, characterising the trend model.

Discussion

Although approximately the same number of individuals was identified annually in the two transient killer whale populations we monitored in the coastal waters of Prince William Sound and the Kenai Fjords, the population parameters estimated by our mark recapture model were notably different. The AT1 transients exhibited high site fidelity and high capture probability, indicating that essentially every member of this small population was photographed annually in our coastal study area. In contrast, we estimated higher rates of turnover and lower capture probabilities in the study area for GOA transients. The most likely explanation for the latter pattern is that these whales were part of a significantly larger population with a more extensive range. The distribution of sightings was heavily weighted toward the ocean entrances and outer coast

Table 2

Photographic resighting date and location data of Gulf of Alaska (GOA) transient killer whales (*Orcinus orca*) in coastal southeastern Alaska (SEA) and British Columbia (BC).

Year	Month	Day	Region	Location	Latitude N	Longitude W	GOA whales identified
1995	3	24	SEA	Sitka Sound	56°58′	135°33′	AT74
1997	11	5	SEA	Sitka Sound	57°0′	135°20′	AT70 AT71 AT72 AT73 AT73A AT75
1997	2	4	SEA	Sitka Sound	56°58′	135°33′	AT74
1997	1	9	SEA	Sitka Sound	56°58′	135°33′	AT74
1998	7	19	SEA	Glacier Bay	58°28′	136°1′	AT30 AT32
2000	3	10	SEA	Sitka Sound	57°6′	135°28′	AT70 AT71 AT72 AT73 AT75 AT80
2000	4	4	SEA	Sitka Sound	57°1′	135°21′	AT72 AT70 AT71 AT75 AT73 AT80
2001	6	5	SEA	Glacier Bay	58°28′	136°1′	AT30 AT32 AT74 AT74A
2001	7	23	BC	Skaat Harbor	52°24′	131°26′	AT30 AT32
2002	2	24	SEA	Sitka Sound	57°7′	135°31′	AT70 AT71 AT72 AT73 AT75 AT80
2003	2	28	SEA	Sitka Sound	56°55′	135°39′	AT74 AT74A
2003	3	2	SEA	Sitka Sound	56°55′	135°39′	AT74 AT74A
2004	5	16	BC	Hecate Strait	53°54′	131°0′	AT74 AT74A
2007	2	7	SEA	Sea Lion Rock	57°17′	135°57′	AT70 AT71 AT75
2007	2	19	SEA	Yasha Island	56°57′	135°35′	AT74 AT74A
2007	7	19	SEA	Glacier Bay	58°34′	136°6′	AT141, AT142, AT143

Table 3

Summary of attachment and movement data for satellite tags placed on Gulf of Alaska (GOA) and AT1 transient killer whales (*Orcinus orca*)

Population	Whale	First transmission date	Last transmission date	Duration (days)	Distance (km)	Range (km^2)
GOA	AT109	7/4/2007	7/20/2007	17	1528	18415
GOA	AT73	9/20/2008	10/19/2008	30	3839	270503
GOA	AT122	6/12/2010	7/1/2010	19	1115	36222
GOA	AT73	9/21/2010	9/27/2010	7	625	2615
AT1	AT9	8/17/2010	8/22/2010	5	473	3982

for the GOA transients, whereas the AT1 transients were regularly encountered well inside Prince William Sound and Kenai Fjords, including glacial fjords headed by active glaciers (Fig. 1B).

Our trend analysis revealed an abrupt decline in the abundance of the AT1 transient population after the *Exxon Valdez* oil spill in 1989, corroborating earlier interpretations of photo-identification data (Matkin et al., 2008). This decline in abundance correlates with a spike of lower apparent survival from 1989 through 1990 and is almost certainly due to mortality, as supported by the low estimated rates of temporary emigration, high capture probabilities, and the lack of evidence of movement into other areas (Matkin et al., 1999, 2008). The AT1 population is currently exceptionally small at seven individuals, and the lack of recruitment since 1984 indicates their eventual extinction. Although the AT1 population appears to be a remnant group of predators of near-coastal harbor seal (*Phoca vitulina)* and Dall's porpoise (*Phocoenoides dalli*) (Saulitis et al., 2000, 2005), their descent toward extinction was compounded by mortality after the oil spill. Additionally, harbor seals, a primary prey for AT1 killer whales, have declined substantially in our study area during the study period (Frost et al., 1999; Allen and Angliss, 2010).

There was no detectable decline in the GOA transient abundance over the period of study. As occasional visitors to the Prince William Sound–Kenai Fjords region, and because of their more extensive range (as supported by tagging data, Fig. 7A), they have likely been less affected by local changes to habitat and prey. Moreover, the documented prey items of GOA transients are notably different from those of the AT1 transients and include Steller sea lion (*Eumetopias jubatus*) (Saulitis et al., 2000; Heise et al., 2003; Maniscalco et al.,

2007). Maniscalco et al. (2007) found Steller sea lions to be the dominant prey, at least during the non-winter periods in the Kenai Fjords region. Recent observations of GOA transients in southeastern Alaska, described in this article, indicate increased use of that region where, perhaps not coincidentally, Steller sea lion and harbor seal numbers have increased substantially in recent decades (Allen and Angliss, 2010).

The combined numbers of both GOA and AT1 transients that used Prince William Sound and Kenai Fjords over the course of a season was very low (currently estimated at ~16 whales in 2010) when compared with adjacent areas. In contrast, the parapatric west coast transient population in the coastal waters of southeastern Alaska, British Columbia, and Washington State numbers more than 200 individuals (Ford et al., 1999). Also, an annual aggregation of 80–100 transient whales has been reported in the Unimak Island region of the eastern Aleutian Islands in May and June (Matkin et al., 2007; Barrett-Lennard et al., 2011), and more than 300 transients use the coastal waters of a broader region of the Gulf of Alaska and Aleutian Islands (Durban et al., 2010). These differences likely reflect lower prey availability for mammal-eating killer whales in the northern Gulf of Alaska compared with adjacent regions.

Nuclear genetic diversity (Barrett-Lennard, 2000) indicates that the AT1 transients were once a much larger population. This, coupled with their more recent sharp decline, makes it unlikely that predation by these whales was a significant factor in dramatic decline of harbor seals in Prince William Sound in recent decades. Although it is conceivable that AT1 predation may have slowed harbor seal recovery, it is possible that the recent rebound in harbor seal numbers in Prince William Sound benefited from the AT1 decline. In the ten-year period 1997–2006, harbor seal numbers increased an average of 1.66% per year (95% confidence interval=0.34% , 2.98% per year) (Small[3]).

Maniscalco et al. (2007) suggested that Steller sea lions were a primary prey for GOA transients in Kenai Fjords, at least seasonally, and that the small number of transients that used the area was not likely to have caused a decline in Steller sea lions. The consistent low numbers and lack of apparent increase in use of the area by GOA transients found in our study argue for a relatively even predation pressure on Steller sea lions in recent decades and support the conclusions of Maniscalco et al. (2007). In our population analysis we find little support for the hypothesis that declines in harbor seals or Steller sea lions in Prince William Sound and Kenai Fjords were a direct result of pre-

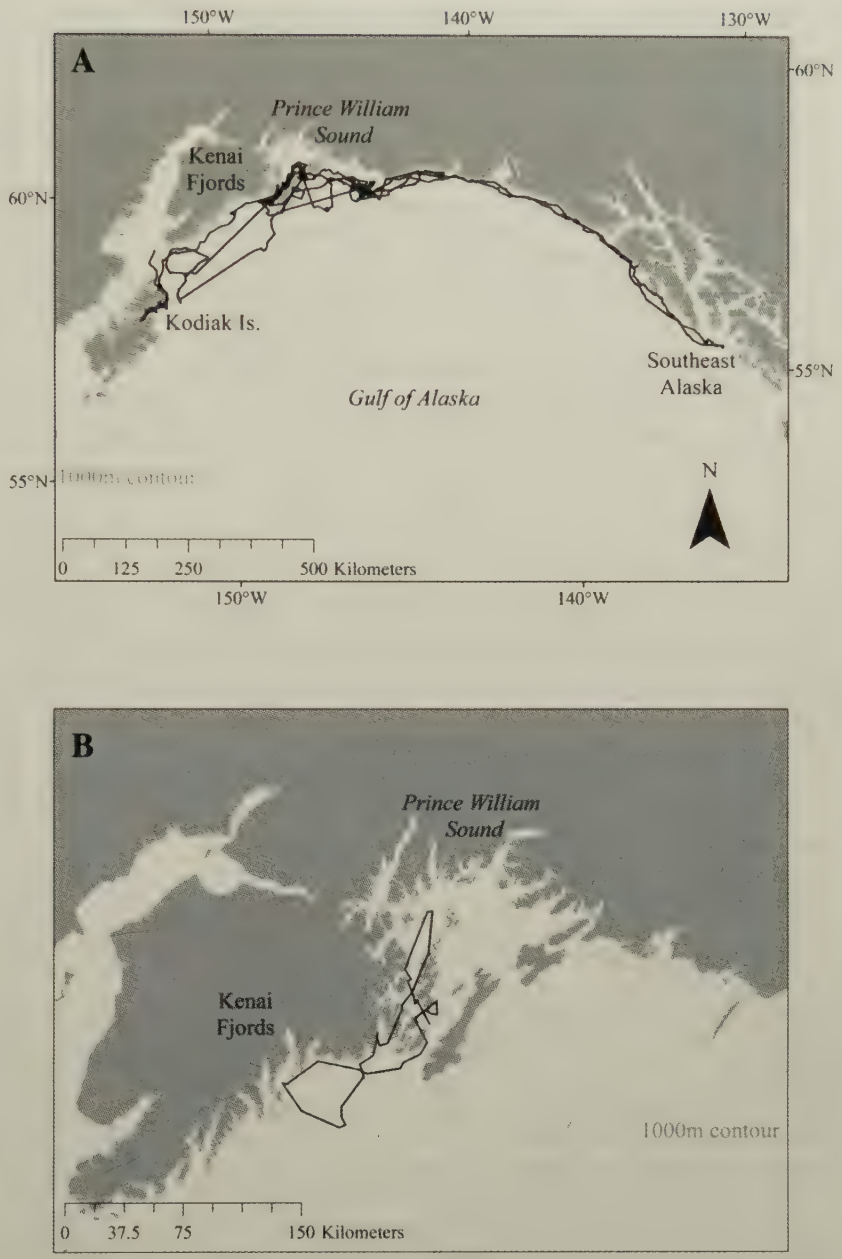

Figure 7

Map of filtered movement tracks of (**A**) Gulf of Alaska (GOA) (4) and (**B**) AT1 (1) transient killer whales (*Orcinus orca*) tagged with a low impact minimally percutaneous external-electronics transmitter (LIMPET) and subsequently tracked in 2007–10 as summarized in Table 3.

[3] Small, R. 2010. Personal commun. Alaska Department of Fish and Game, Juneau, Alaska 99802.

dation pressure by an increased number of transient killer whales.

It might be expected that the combination of reduced numbers of AT1 transient whales, the apparent rebound of harbor seals in the region, and a recent increase in Steller sea lion numbers, particularly in the eastern Gulf of Alaska (Allen and Angliss, 2010), would lead to increased use of these coastal waters by GOA transients. Because the local extinction of a killer whale population, as is likely for the AT1 population, is an unprecedented event, it is unknown whether members of the GOA population eventually will expand their use of the region. Our analysis indicates that, despite greatly reduced AT1 transient numbers and a slowly increasing prey population, this has not yet occurred.

Conclusion

This study illustrates the importance of examining differing population trends and movements of individual killer whale ecotypes to reveal subtleties of population ecology and potential prey impacts. The Kenai Fjords–Prince William Sound region at the northern Gulf of Alaska supports two distinct non-associating transient populations that both occur at low numbers relative to other well-studied North Pacific regions. Despite their common position at the apex of marine food chains, each population exerts unique ecological impacts based on food preferences, prey abundance, and habitat use. These diverse impacts are reflected in the different range and trajectories of our study populations. The AT1 transients are a localized, inshore population apparently headed for extinction, whereas the GOA transients are a wider ranging, more oceanic population with relatively stable numbers.

Our study reveals that for small, infrequently observed populations such as the GOA transients, mark-recapture methods can be coupled with a Bayesian statistical approach to quantify important population parameters and examine population trends. With a combination of extensive geographically based photographic data and satellite tracking results, we can begin to define important aspects of population ecology.

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A comparison between circle hook and J hook performance in the dolphinfish, yellowfish tuna, and wahoo troll fishery off the coast of North Carolina

Paul J. Rudershausen (contact author)[1]
Jeffrey A. Buckel[1]
Greg E. Bolton[2]
Randy W. Gregory[3]
Tyler W. Averett[1]
Paul B. Conn[4,5]

Email address for contact author: pjruders@ncsu.edu

[1] Department of Biology
Center for Marine Science and Technology
North Carolina State University
303 College Circle
Morehead City, North Carolina 28557

[2] North Carolina State University
Department of Food, Bioprocessing, and Nutrition Sciences
Center for Marine Science and Technology
303 College Circle
Morehead City, North Carolina 28557

[3] North Carolina Division of Marine Fisheries
3441 Arendell Street
Morehead City, North Carolina 28557

[4] National Marine Fisheries Service
Southeast Fisheries Science Center
101 Pivers Island Road
Beaufort, North Carolina 28516

[5] National Marine Fisheries Service, NOAA
National Marine Mammal Laboratory
Alaska Fisheries Science Center
7600 Sand Point Way NE
Seattle, Washington 98115-6349

Abstract—We compared numbers of strikes, proportions of fish that hooked up after strikes, proportions of fish that stayed on hook (retained) after hook up, and numbers of fish caught between circle and J hooks rigged with dead natural fish bait (ballyhoo) and trolled for three oceanic predator species: dolphinfish (*Coryphaena hippurus*), yellowfin tuna (*Thunnus albacares*), and wahoo (*Acanthocybium solandri*). Interactions were compared between circle and J hooks fished on 75 trips by two user groups (charter and recreational fishermen). Hooks were affixed to three species-specific leader types most commonly fished in this region: monofilament (dolphinfish), fluorocarbon (tuna), and wire (wahoo). Numbers of fish caught per trip and three potential mechanisms that might influence numbers caught (i.e., number of strikes, proportion of fish hooked, and proportion retained) were modeled with generalized linear models that considered hook type, leader type, species, user (fishing) group, and wave height as main effects. Hook type was a main effect at the catch level; generally, more fish were caught on J hooks than on circle hooks. The effect of hook type on strike rates was equivocal. However, J hooks had a greater proportion of hook-ups than did circle hooks. Finally, the proportion of fish retained once hooked was generally equal between hook types. We found similar results when data from additional species were pooled as a "tuna" group and a "mackerel" group. We conclude that J hooks are more effective than circle hooks at the hook-up level and result in greater numbers of troll-caught dolphinfish, tunas, and mackerels.

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Literature on a variety of species and fishing strategies provides evidence that catch rates with circle hooks can be maintained (but rates of deep hooking are reduced) when compared with catch rates with conventional J hooks (Cooke and Suski, 2004). Studies on the relative effectiveness of hook types for billfishes have revealed that circle hooks offer a conservation benefit (reduced rates of deep hooking) while maintaining catch rates comparable to those with J hooks for both troll and longline fisheries (Serafy et al., 2009). For example, Prince et al. (2002) found that trolled circle hooks rigged with natural baits maintained catch rates of Atlantic sailfish (*Istiophorus platypterus*) but reduced rates of deep hooking compared with catch rates with J hooks. Similarly, Horodysky and Graves (2005) found that white marlin (*Kajikia albida*) caught on trolled circle hooks had no mortality compared to 35% mortality on J hooks. Based on these findings, a rule was instituted by the National Marine Fisheries Service (NMFS) that required the use of non-offset circle hooks when trolling natural or combination baits (natural bait and skirt) in Atlantic billfish tournaments (Federal Register, 2006). The intent of this regulation was to reduce deep hooking, and thus rates of catch-and-release mortality, in white and blue marlin (*Makaira nigricans*).

Outside of directed tournaments, Atlantic billfishes are generally not the only targets in charter and recreational troll fishery of North Carolina. For many ports, billfishes are only a rare bycatch. In North Carolina, dolphinfish (*Coryphaena hippurus*), yellowfin tuna (*Thunnus albacares*), and wahoo (*Acanthocybium solandri*) are the predominant targets of recreational and charter trip troll fisheries in Gulf Stream waters (senior author, personal observ.). Dolphinfish and yellowfin tuna are the top two species by weight landed in the North Carolina recreational fishery and together represent over half of the total recreational landings in the state (NCDMF, 2010). Recreational and charter anglers harvest 93% of the roughly 4.5 million kg of dolphinfish landed annually along the U.S. Atlantic coast and roughly 90% of wahoo landed in U.S. South Atlantic waters (North Carolina through Florida) and Mid-Atlantic waters (New York through Virginia) (SAFMC, 2003). Trolling is the predominant fishing method for pelagic fishes in Gulf

Stream waters off of North Carolina. Catch composition of dolphinfish, yellowfin tuna, and wahoo in this troll fishery varies widely among vessels, seasons, and locations in the Gulf Stream.

There is concern in the charter boat industry that circle hook regulations (developed for and based on billfish), if ever mandated outside of U.S. Atlantic billfish tournaments, would negatively impact catch rates of dolphinfish, yellowfin tuna, and wahoo. Chartering an offshore fishing trip in the southeastern United States is an expensive endeavor (~$2000/day; senior author, personal observ.) and reductions in catch may have economic influences on charter fishing businesses. Success of the offshore troll fishery relies on clientele having a reasonable chance to catch and keep fish that are highly valued as seafood. In North Carolina, there are few charter captains willing to use or experiment with circle hooks when targeting non-billfish species because there is a widespread perception that trolling circle hooks for non-billfish species results in reduced catch rates, and therefore greater chances for customer dissatisfaction, compared with J hooks. The charter ocean fishing industry in North Carolina includes roughly 750 vessels and receives $65 million annually in for-hire fees (Dumas et al., 2009). Economic ramifications of requiring circle hooks outside U.S. Atlantic billfish tournaments have not been quantified.

Our purpose in undertaking this study was to determine the effects of using circle hooks on catch levels of non-billfish species in the U.S. southeastern offshore troll fishery in comparison with catch levels with J hooks. Mechanisms that might explain differences or similarities in catch between hook types were also examined. Questions were the following: 1) Did predators strike circle and J hook rigged baits at similar rates?; 2) Once struck, did circle and J hook rigged baits have similar proportions of hook-ups?; and 3) Once hooked up, did circle and J hook rigged baits have similar proportions of retained fish (brought to the boat)?

Materials and methods

Fishing techniques workshop

In November 2007 we convened a workshop attended by state and federal biologists, fishery managers, charter boat captains and mates, private boat anglers, and billfish tournament directors. The purpose of the workshop was to select hook types, hook styles, rigging techniques, and fishing techniques (see below) that could be used to compare trolled circle and J hooks in Gulf Stream waters off North Carolina during troll fishing days aboard charter vessels.

Defining and selecting circle and J hooks was a central part of the workshop. A circle hook was defined as having the point perpendicular to the hook shank. A J hook was defined as having the point and point shank parallel to the hook shank. We selected circle and J hooks that would be comparable in bend diameter (gap between hook shank and point shank). For both hook types, we selected barbed hooks with zero offset and straight hook eyes (eye parallel to the hook shank). The circular shape, hook point turned perpendicularly toward the shank, and zero offset insured that the circle hooks we selected conformed to the National Marine Fisheries Service definition in the current billfish tournament regulations (Federal Register, 2006). Other hook characteristics (hook size, hook gauge, gap width, and shape) were selected to avoid compromising the action and durability of the trolled dead whole fish (ballyhoo [*Hemiramphus brasiliensis*]). Participants decided that circle and J hooks with a gap width large enough that allowed space between the bait and hook for hooking fish but with a relatively low profile (by virtue of the gauge of hook wire) would be most appropriate for testing.

Bait rigging and fishing techniques

The bait rigging techniques for each non-billfish species presented at the workshop were those used by the local charter industry. Circle and J hooks were embedded in ballyhoo except for directed trips for dolphinfish, when circle hooks were rigged externally (Fig. 1). Other differences in bait rigging and fishing techniques are described below by species. Hook sizes and styles, leader characteristics, and rigging techniques differed slightly on recreational trips because these fishermen often troll with smaller hooks and different rigging techniques from those used by charter captains.

For charter and recreational trips targeting dolphinfish we used Mustad 9175 7/0 J hooks (Mustad, Gjövik, Norway[1]) that were rigged inside ballyhoo; the chin weight was affixed to 30 cm of rigging wire. We used Eagle Claw 2004ELG 8/0 circle hooks (Eagle Claw Fishing Tackle Co, Denver, CO) rigged externally to the ballyhoo with a 7-g chin weight and swivel at the top of the head, with 30-cm of rigging wire (no pin). The leader was 1.8 m of 36 kg of monofilament attached to the standing line with a 31-kg Sampo ball-bearing swivel (Sampo Inc., Barneveld, NY). The leader was attached to the hook by using a loose crimp with tag end opposite the point (Fig. 1A). We used lever drag reels affixed to "thirty pound-class" stand-up rods at all locations. Reels were spooled with a 14-kg test Diamond® monofilament line (Diamond Fishing Products, Pompano Beach, FL). The drag upon strike of a fish was set just above "free spool" (reel gear not engaged) with the clicker in the "on" position. The drag during the fight of a fish (regardless of species) was roughly 6.4 kg. Baits were dropped back (line allowed to come off the spool with no drag) to missed fish (that struck) immediately after the strike. Recreational rigging techniques for dolphinfish were similar to those used on the

[1] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

charter vessel except that 1) circle and J hooks were one size smaller.

Charter trips targeting yellowfin tuna used Mustad 7692 9/0 J hooks and Eagle Claw 2004ELG 9/0 circle hooks rigged inside ballyhoo, with 7-g chin weights affixed to a pin. Hook and leader were secured to the bait with a rubberband (for wahoo see next paragraph). The leader was 9 m of 36 kg of clear fluorocarbon leader through which a blue and white Seawitch lure (C&H Lures, Jacksonville, FL) with a 14-g lead head was threaded and positioned above the eye of the hook (Fig. 1B). The leader was attached to the standing line with a 36-kg SPRO power swivel (SPRO Corp., Kennesaw, GA). Both hook types were attached to the leader with a loose crimp with the tag end opposite the point. We used Penn "50-wide" reels (Penn, Philadelphia, PA) affixed to "fifty pound class" stand-up rods at all locations. Reels were spooled with 27-kg Diamond® line. The drag upon strike was set at roughly 4.5 kg while the drag during fight (regardless of fish species) was set to roughly 6.4 kg. Baits were dropped back to missed strikes and then only until a fish picked up the bait.

Figure 1

Circle and J hook rigging techniques and leader types used in trolling ballyhoo for (**A**) dolphinfish (*Coryphaena hippurus*) on monofilament leaders, (**B**) yellowfin tuna (*Thunnus albacares*) on fluorocarbon leaders, and (**C**) wahoo (*Acanthocybium solandri*) on single-strand wire leaders. The circle hook is the bottom hook type in each of the three photographs.

Recreational rigging techniques for yellowfin tuna were similar except that 1) circle hooks were the same type and style but one size smaller, 2) J hooks were Mustad 3407, 7/0 size, 3) the fluorocarbon leader was 3.7 m long, and 4) "thirty pound class" stand up rods were used.

Charter trips targeting wahoo used Mustad 7731A 8/0 J hooks and Eagle Claw 2004 ELG 9/0 circle hooks rigged inside ballyhoo with a 7-g chin weight and pin that comprised part of the wire leader. The leader was 3.7 m of #9 (41 kg) piano wire (Fig. 1C) with haywire twists for attaching leader to a hook at one end and for forming a loop at other end; the leader was attached to the standing line with a 59-kg ball bearing clip swivel. As with yellowfin tuna, a blue and white Seawitch lure with a 14-g lead head was threaded through the leader and positioned above the eye of the hook. The same rod and reel types used for yellowfin tuna were used for wahoo. Baits were dropped back to missed strikes and then only until a fish picked up the bait. Recreational rigging techniques for wahoo were similar to those used for charter fishing except that 1) circle hooks were one size smaller; 2) J hooks were Mustad 3407, 7/0 size and 3) "thirty pound class" stand up rods were used.

Data collection

Circle and J hooks were trolled side-by-side for both the charter and recreational groups. Fishing occurred in Gulf Stream and nearby ocean waters off North Carolina. The two charter boats were employed in order to simulate a typical for-hire fishing operation in this region. Each of the two captains and mates used for charter trips in this study had over 20 years experience in this fishery, as well as experience rigging and trolling circle hooks for billfishes. Fishing aboard a research vessel was conducted to simulate a recreational operation where fishermen have no mate to coordinate the fishing operation (i.e., to coordinate, rig, and check baits; monitor and clear lines; check drags; and hook

and gaff fish), but instead do these activities themselves. Before each charter trip, the captain and first author determined which non-billfish species would be targeted and adjusted the tackle class, leader, and rig type accordingly; the first author made this determination for the recreational trips. This determination was based on water temperature, time of year, and fishing reports that indicated which species we would be most likely to interact with. We fished monofilament, fluorocarbon, and wire leaders a total of 6, 12, and 18 days on the charter vessels, and 18, 7, and 14 days on the recreational vessel. There were not equal numbers of days fished between the two user groups. At most, one boat trip was taken per day.

On each of the two charter vessels we fished pairs of standing rods (held by fixed rod holders) from four positions. These four pairs were flat lines, short outriggers (riggers), long riggers, and bridge poles. On windy days, rods were not fished from the bridge because of increased likelihood of tangles in the lines. On days directed for wahoo, we used in-line planers on the flat-line rods in order to fish baits deeper in the water column and elicit a greater number of interactions with this species. We randomly selected which side of the boat (port or starboard) would receive the circle and J hook treatment on each day of charter fishing.

We fished two pairs of lines simultaneously aboard the research vessel. These pairs were flat lines and poles fished from rod holders on a canopy "t-top." For each day of fishing on the recreational vessel, we staggered hook types so that a hook type on a flat line was on the side of the boat opposite that same hook type on the t-top.

The three vessels used to collect data trolled at between six and seven knots (regardless of species targeted). Chains of combined artificial lures consisting of four 23-cm long squids ending with a blue and white Iland Lure® (L&S Bait Company, Inc., Largo, FL)-ballyhoo bait combination were deployed as teasers (no hooks) from each vessel during the collection of data. A chain of pink squids was deployed on the starboard side of the boat and a chain of green squids was deployed on the port side of the boat. Baits were medium ballyhoo that were replaced upon washout.

We recorded fish total length (mm) when it was possible to associate a fish length with a hook type. This was not always possible because of multiple fish being caught and placed in fish box at nearly the same time. Hooking location was recorded for all captured fish.

Data analysis

Four response variables were measured: numbers caught, numbers of strikes, proportion hooked up, and proportion retained. Numbers of fish caught reflected the cumulative results for the strike, hook-up, and retention levels. A fish interacting with the gear in a manner such that the line was pulled from the outrigger clip or that engaged the reel clicker when no clip was used was considered a strike (Prince et al., 2002). A fish that had been hooked for 10 seconds after striking was considered a hook-up. A retained fish was one where the leader was touched or the fish put into the boat ("boated"). The proportion of fish that hooked up was relative to the number that struck (Prince et al., 2002); similarly, the proportion of fish that were retained on the hook was relative to the number that hooked up.

Strikes and hook-ups for fish not caught or visually identified were included in the analysis. When the appearance of a struck bait (e.g., bite marks), water temperature, time of year, fishing location, fish behavior (jumping), and order of fish landed each day indicated a particular species, we attributed these interactions to that species. When these six factors did not combine to indicate a particular species, these interactions were considered to be from an unidentified species. We allocated strikes and hook-ups from unidentified fish to each species in the same proportion as that for fish boated for that day of fishing. At each level of interaction we found similar best fitting models for data that excluded or included unidentified fish (Rudershausen et al., 2010).

Generalized linear models (GLMs) were used to determine the effects of hook type (circle or J), leader type (monofilament, fluorocarbon, or wire), species (dolphinfish, yellowfin tuna, or wahoo), user group (recreational or charter), wave height, and potentially important interactions on the numbers of fish caught and each of three mechanisms leading to a caught fish. We constructed a sequence of Poisson GLMs for the numbers caught and numbers of strikes data sets. For hook-up and retention data, we used binomial GLMs to represent the conditional nature of the hook-up and retention processes (e.g., the number of fish that hooked up in a given trip was conditional on the number that struck). In each case, hook type, leader type, species, and user group were treated as categorical variables, whereas wave height was treated as a continuous variable. Species caught on days where they were not the main target were included in all analyses and are referred to as "nondirected" species. At each level of interaction, plots were constructed to help better visualize the relative effectiveness of circle and J hooks on directed leader types.

We collected the same response variable data for other species that have feeding styles similar to those of yellowfin tuna and wahoo to provide additional data to clarify trends in relative hook-type effectiveness. The four model sets described above were also fitted to data sets that included blackfin tuna (*Thunnus atlanticus*), skipjack tuna (*Euthynnus pelamis*), and false albacore (*Euthynnus alletteratus*), which were combined with yellowfin tuna data to form a "tuna" group (family Scombridae, tribe Thunnini), and king mackerel (*Scomberomorus cavalla*) and Spanish mackerel (*Scomberomorus maculatus*), which were combined with wahoo data to form a "mackerel" group (family Scombridae, tribe Scomberomorini). This additional model fitting kept dolphinfish as a single-species group.

We adopted an information-theoretic perspective to compare the parsimony of relatively simple models

that we believed would help determine relative effectiveness of each hook type at catching fish and on mechanisms during the fish-hook interaction (strike, hook-up, and retention). We inspected data plots to determine factors other than hook that contributed to variability in catch rates. Base models for each level of fish interaction were then constructed without hook main effects and hook interactions. For each of these potential base models we calculated a quasi-Akaike's information criterion (QAIC; Burnham and Anderson, 2002). QAIC was computed instead of AIC because of potential over-dispersion of the data used as the response variable in each model (Burnham and Anderson, 2002). At each level of fish interaction, we selected the base model with the lowest QAIC value. The most parsimonious base models had 1) main effects (excluding hook) plus a leader-species interaction at the catch level; 2) main effects (excluding hook) plus leader-species and species-user interactions at the strike level; 3) main effects (excluding hook) plus a leader-user interaction at the hook-up level; and 4) main effects (excluding hook) plus a species-user interaction at the retention level. After the base model was selected, we developed incrementally more complex models that then included a hook effect and interaction terms between hook and other factors. This sequential model building allowed us to determine if the main factor of interest—hook type—covaried with other factors potentially influencing interactions with fishes. Any models with three-way interactions also included two-way subinteractions. $QAIC_i$ values were then used to compare fits among all i models (including the base model) at each level of fishing interaction to help determine the combination of predictors that best explained variation in the data. The ΔQAIC value for each model was calculated as the difference between any particular model ($QAIC_i$) and the minimum QAIC for the best fitting model in the set ($QAIC_{min}$). The model with the $QAIC_{min}$ value was, for each model set, considered to be the one representing the data adequately with the fewest parameters; however, we regarded models that differed by <~ 4 ΔQAIC as all having reasonable support (Burnham and Anderson, 2002). We also computed Akaike weights (w_i) for each model to help gauge the relative support for each model in the model set; the value of w_i varies between 0 and 1, with a greater value indicating that a particular model better fits the data. See Burnham and Anderson (2002) for equations used to compute QAIC and w_i.

Highly parameterized models often resulted in singular Hessian matrices, indicating that one or more parameters were nonidentifiable. However, we retained these models in each model set because our primary goal was to obtain parsimonious predictions of how hook type affected catch rates. In an information-theoretic context, over-parameterized models would simply be penalized for requiring additional parameters to explain the same amount of variation in the data and therefore would be unlikely to be selected with QAIC.

The selection of base models and development of more complex models incorporating a hook main effect and hook interactions by using data on taxa (e.g., dolphinfish, "tunas," and "mackerels") followed the process used for the three species. Base models at each level of fish interaction were the same as in the species analyses described above with the exception of the retention level, where a model consisting of main effects (except hook) plus a leader-species interaction best fitted the taxa data.

We computed the relative effectiveness of circle and J hooks (effect size) by comparing predicted circle and J hook catch rates of dolphinfish, yellowfin tuna, and wahoo on their respective directed leader types. Effect size was calculated for each catch model with a positive Akaike weight (w_i) (see *Results* section). Effect size (ES) for each of these models was computed as

$$ES = \frac{\mu_x}{\mu_y}, \quad (1)$$

where μ_x and μ_y = the predicted mean catch-per-trip values on circle and J hooks, respectively.

Effect size theoretically ranges from zero to greater than one. An effect size less than, equal to, or greater than one indicates that circle hooks are less, equally, or more effective than J hooks, respectively. The variance (σ^2) about each effect size was calculated as

$$\sigma^2 = \frac{\sigma_x^2}{\mu_y^2} + \frac{\left(\mu_x^2\right)\left(\sigma_y^2\right)}{\mu_y^4}, \quad (2)$$

where σ_x^2 and σ_y^2 are the variances about the mean predicted mean catch-per-trip values of circle and J hooks. The values for user and wave were held constant (at 0.48 and 0.79 m, respectively) when computing effect size for the three species-leader combinations from each aforementioned catch model. The effect size from each model was weighted by the relative w_i value. Weighted effect size values from each model were summed to determine an overall effect size for each of the three species caught on its directed leader type. This model-averaging procedure was repeated to compute overall variance about each average effect size; model averaging for variance was conducted by multiplying each model's variance by the squared value of the Akaike weight (w_i^2). Computations of predicted effect sizes and associated variances were repeated with the data on taxa.

For each species, we compared median lengths between hook types with a median ranks test (α=0.05). Data were combined across leader types and user groups for each of these size-based analyses. For each species, we compared rates of jaw (mouth) and deep hooking (gut, gills, or eyes) among hook types using a chi-square square test of independence.

Table 1

Number of fish caught on circle and J hooks from 39 recreational and 36 charter trips trolling both hook types with natural and combination baits offshore of North Carolina, 2006–10. Each number (no.) and percent (%) column is specific to user group (recreational vs. charter) and hook type (circle vs. J). Each column of % values adds up to 100%.

	Recreational				Charter			
	Circle		J		Circle		J	
Species	No.	%	No.	%	No.	%	No.	%
Dolphinfish (*Coryphaena hippurus*)	35	63.6	71	77.2	45	40.2	73	38.8
Yellowfin tuna (*Thunnus albacares*)	7	12.7	5	5.4	25	22.3	47	25.0
Wahoo (*Acanthocybium solandri*)	0	0.0	1	1.1	20	17.9	22	11.7
Blackfin tuna (*Thunnus atlanticus*)	0	0.0	0	0.0	14	12.5	26	13.8
King mackerel (*Scomberomorus cavalla*)	8	14.5	3	3.3	0	0.0	4	2.1
Barracuda (*Sphyraena barracuda*)	1	1.8	0	0.0	1	0.9	3	1.6
Spanish mackerel (*Scomberomorus maculatus*)	0	0.0	3	3.3	0	0.0	0	0.0
False albacore (*Euthynnus alletteratus*)	2	3.6	6	6.5	4	3.6	5	2.7
Greater amberjack (*Seriola dumerili*)	0	0.0	1	1.1	0	0.0	1	0.5
Bluefish (*Pomatomus saltatrix*)	0	0.0	1	1.1	0	0.0	0	0.0
Atlantic sailfish (*Istiophorus platypterus*)	1	1.8	0	0.0	2	1.8	4	2.1
White marlin (*Tetrapturus albidus*)	0	0.0	1	1.1	0	0.0	0	0.0
Blue marlin (*Makaira nigricans*)	0	0.0	0	0.0	0	0.0	1	0.5
Skipjack tuna (*Euthynnus pelamis*)	0	0.0	0	0.0	1	0.9	2	1.1
Bullet mackerel (*Auxis* spp.)	1	1.8	0	0.0	0	0.0	0	0.0

Results

Catch composition

The three most abundant species captured on recreational trips were dolphinfish, yellowfin tuna, and king mackerel, which together constituted 91% of the catch on circle hooks and 86% on J hooks. The three most abundant species captured on charter trips were dolphinfish, yellowfin tuna, and wahoo, which together constituted 80% of the catch on circle hooks and 76% on J hooks. Blackfin tuna were commonly caught on charter trips, constituting 13% of the catch on circle hooks and 14% of the catch on J hooks. Billfishes made up 1% of the catch on recreational trips and 3% of the catch on charter trips (Table 1). Pooling across both user groups, we found that 74% of dolphinfish were caught on monofilament leaders, 96% of yellowfin tuna were caught on fluorocarbon leaders, and 98% of wahoo were caught on wire leaders; that is, the vast majority of individuals from each species were captured on the respective directed leader type. Species identity could not be determined in 14.0% of strike and 2.9% of hook-up interactions over the course of the study.

Comparisons of catch and examination of mechanisms influencing catch

Hook type influenced catch rate (Fig. 2). For the three-species analysis of catch rate, the base model plus a hook main effect received majority support (Table 2). For directed leaders, J hooks caught more dolphinfish than circle hooks for both recreational and charter groups. Higher catches on J hooks were also observed in the charter group for yellowfin tuna; however, there was no clear hook effect within the recreational group for yellowfin tuna or wahoo or charter group for wahoo. Partial support for models containing hook-user and hook-species interactions confirms these observations (Table 2). The hook-leader interaction also had support and was most obvious in the dolphinfish data where the hook effect was not consistent across leader types (Fig. 2). Model fitting to numbers-caught data with taxa (i.e., dolphinfish, tunas, and mackerels) provided similar results to those for species data (Table 2; Fig. 3); the base model plus a hook main effect received majority support as the best fitting model and models that included hook-user, hook-leader, and hook-species interactions had QAIC values within four units of the best fitting model. Tunas were caught more often on J hooks and fluorocarbon leaders than other hook-leader combinations. Mackerels were caught slightly more often on J hooks than circle hooks, and most often on wire leaders (Fig. 3).

The first mechanism contributing to catch was strike. Hook type had little effect on strikes for each of the three species examined (Fig. 4). No single model received majority support when fitted to strike data for the three species and the base model with a hook factor received only slightly greater support than the base model without the hook parameter (Table 3). Models

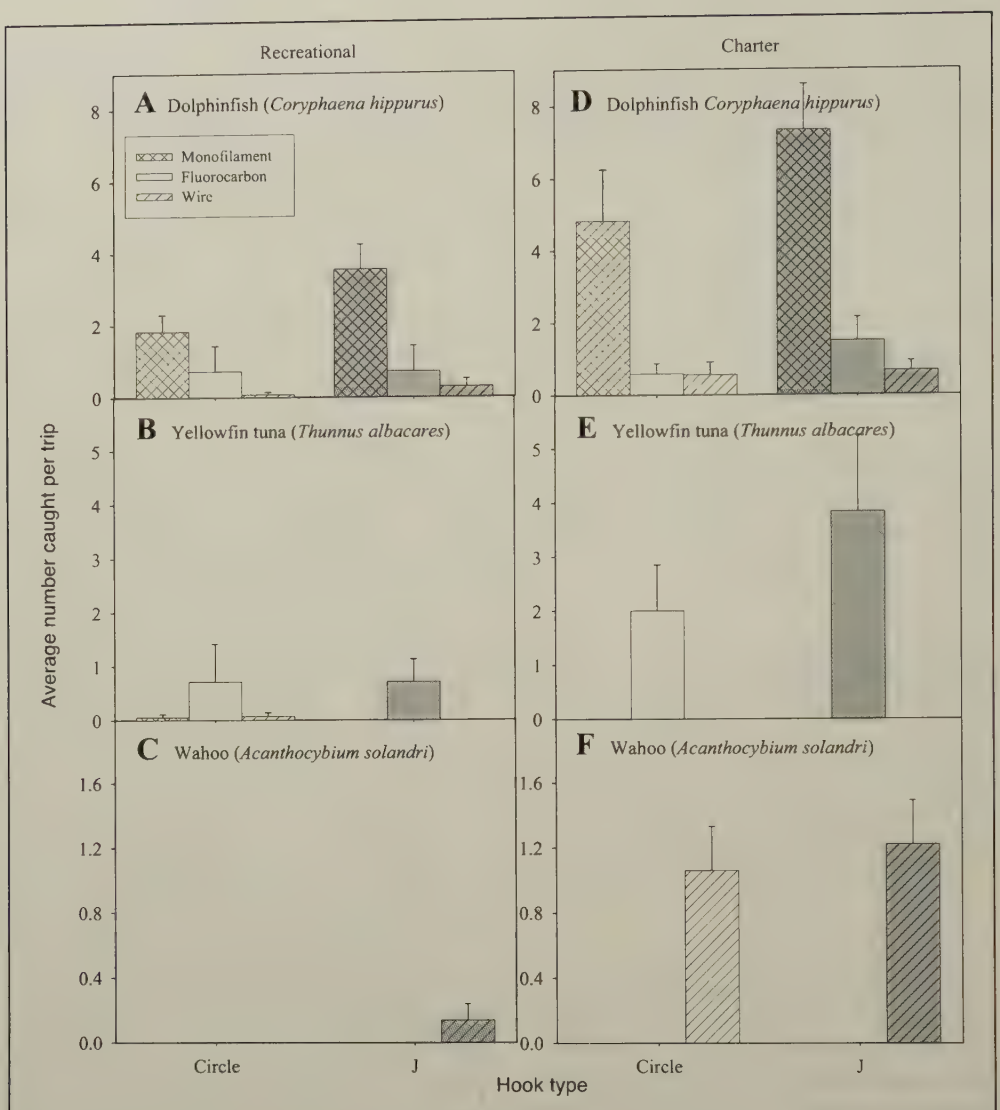

Figure 2

Plots of the average catch per trip (±standard error) on circle hooks (open bars) and J hooks (gray bars). Data for each species are from both directed and nondirected trips for that species. Plots are broken down by user group (recreational [left column, panels **A–C**] and charter [right column, panels **D–F**]) and species (dolphinfish [*Coryphaena hippurus*] [A, D], yellowfin tuna [*Thunnus albacares*] [B, E], and wahoo [*Acanthocybium solandri*] [C, F]). The legend denoting fill pattern for each leader type applies to all panels. No bar for a particular hook-type+species+user-group+leader-type combination indicates no catch.

with hook-user, hook-leader, and hook-species interactions each received a relatively small amount of support. Greater numbers of strikes occurred 1) on charter boats (owing to a greater number of rods fished), 2) when using monofilament leaders, and 3) from dolphinfish than any other species. As with the three species data, there was little difference in the average strikes per trip between circle and J hooks for each taxa (Fig. 5). Similarly, the model that best fitted strike data for the taxa was the base model with hook, but the base model without hook received only slightly less support (Table 3; Fig. 5). Models with hook-user, hook-species, and hook-leader interactions received relatively minor support.

The second mechanism contributing to catch was hook-up. J hooks were more effective at hooking fish for many user group-species combinations (Fig. 6). Hook was a main effect in the model that best fitted the proportional hook-up data (Table 4). Models that received less support included hook-user, hook-species, hook-leader, and hook-species + hook-user interactions. The base model received no support. There was a reduction of hook-ups for dolphinfish when circle hooks were used on both recreational and

Table 2

Candidate models fitted to catch-per-trip data for three species (dolphinfish [*Coryphaena hippurus*], yellowfin tuna [*Thunnus albacares*], and wahoo [*Acanthocybium solandri*], and taxa [dolphinfish, tunas, and mackerels]) when trolling circle and J hooks in Gulf Stream waters off North Carolina. Quasi-Akaike information criterion (QAIC) was used to evaluate model performance, with the lowest value indicating the most parsimonious model. Categorical predictor variables included hook type (hook), leader type (leader), species or taxa, and user group (user). Wave height was used as a continuous predictor variable. K=number of parameters for each model; w=Akaike weight. Base models included all predictor variables with exception of hook and any hook interactions; see *Methods* section for a full description of base models. ΔQAIC values ~<4 were considered models with reasonable support.

Interaction	Data type	Distribution	Model	K	QAIC	ΔQAIC	w
Catch: species	Count	Poisson	base + hook	13	356.77	0.00	0.54
			base + hook + hook*user	14	358.42	1.65	0.23
			base + hook + hook*leader	15	360.49	3.72	0.08
			base + hook + hook*species	15	360.90	4.14	0.07
			base + hook + hook*user + hook*leader	16	361.98	5.21	0.04
			base + hook + hook*species + hook*user	16	362.54	5.77	0.03
			base + hook + hook*species + hook*leader	17	364.91	8.15	0.01
			base + hook + hook*species + hook*leader + hook*species*leader	21	373.59	16.83	0.00
			base	12	385.14	28.37	0.00
Catch: taxa	Count	Poisson	base + hook	13	477.17	0.00	0.55
			base + hook + hook*user	14	479.11	1.94	0.21
			base + hook + hook*leader	15	480.63	3.46	0.10
			base + hook + hook*taxa	15	481.14	3.97	0.07
			base + hook + hook*user + hook*leader	16	482.54	5.37	0.04
			base + hook + hook*taxa + hook*user	16	483.16	5.99	0.03
			base + hook + hook*taxa + hook*leader	17	485.11	7.94	0.01
			base + hook + hook*taxa + hook*leader + hook*taxa*leader	21	493.60	16.43	0.00
			base	12	501.35	24.18	0.00

charter trips. This trend was most pronounced on charter trips for all leader types (Fig. 6). The exception was a slightly greater hook-up rate for yellowfin tuna on circle hooks than on J hooks when fishing fluorocarbon leaders on recreational trips. For the taxa analysis, trends in model fitting to proportional hook-up data were similar to three species (Table 4; Fig. 7); hook was a main effect in the best fitting model and it was a main effect and interaction term in models receiving lesser support. The base model received no support (Table 4). The addition of mackerel data on recreational trips strengthened the trend of greater effectiveness of J hooks in hooking up these taxa on wire, the directed leader type for that group (Fig. 7).

The third mechanism contributing to catch was retention. Hook type did not appear to have a pronounced effect on proportion of fish retained (Fig. 8). For models fitted to species data, the base model received majority support (Table 5). A base model with a hook effect was the only other model receiving support, but it was minor. The proportion retained on circle hooks generally equaled (dolphinfish and yellowfin tuna) or slightly exceeded (wahoo) those retained on J hooks on directed leader types (Fig. 8). Proportional retention data for the taxa also showed that retention was high, with little to no difference between hook types (Table 5; Fig. 9). The base model received majority support and the base model with hook as a main effect received less support. Two other models that received minor support had hook-species and hook-user interactions (Table 5).

Estimates of effect size on catch rates determined from model-averaged predictions showed that J hooks were more effective than circle hooks. This trend held across the species and taxa levels. For the three species, mean predicted effect size (± standard deviation [SD]) for dolphinfish, yellowfin tuna, and wahoo on directed leader types was 0.60 (0.05), 0.60 (0.07), and 0.65 (0.09), respectively (Fig. 10), meaning that circle hooks were roughly 60% as effective as J hooks. For the taxa groups, mean predicted effect size (±SD) for dolphinfish, tunas, and mackerels was 0.62 (0.05), 0.62 (0.06), and 0.67 (0.08), respectively (Fig. 10).

There were no significant between-hook differences in the distribution of lengths for dolphinfish (χ^2=0.973, P=0.324), yellowfin tuna (χ^2=0.003, P=0.958), or wahoo (χ^2=0.068, P=0.795). Thus, hook type was not size selective within a species.

The effect of hook type on deep hooking was species dependent. Rates of deep hooking were significantly less for dolphinfish caught on circle hooks than J hooks (Table 6). However, there was no effect of hook type on proportion of deep-hooked wahoo or blackfin tuna. Rates

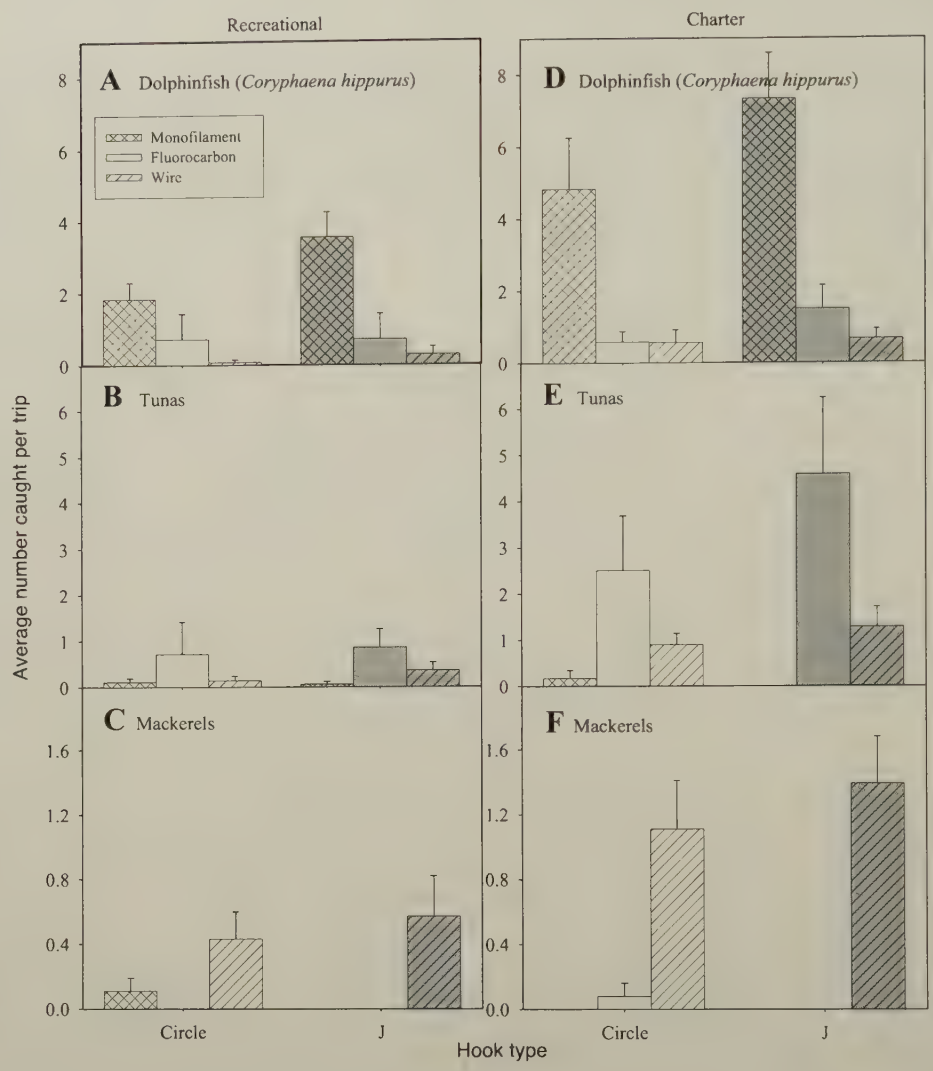

Figure 3

Plots of the average catch per trip (±standard error) on circle hooks (open bars) and J hooks (gray bars). Data for each group are from both directed and nondirected trips for that species. Plots are broken down by user group (recreational [left column, panels **A–C**], and charter [right column, panels **D–F**]), and taxa (dolphinfish *Coryphaena hippurus* [A, D], tunas [B, E], and mackerels [C, F]). The tuna group included yellowfin tuna (*Thunnus albacares*), blackfin tuna (*Thunnus atlanticus*), skipjack tuna (*Euthynnus pelamis*), and false albacore (*Euthynnus alletteratus*). The mackerel group included wahoo (*Acanthocybium solandri*), king mackerel (*Scomberomorus cavalla*), and Spanish mackerel (*Scomberomorus maculatus*). The legend denoting fill pattern for each leader type applies to all panels. No bar for a particular hook-type+taxon+user-group+leader-type combination indicates no catch.

of deep hooking were 0% for both circle and J hooks that caught yellowfin tuna.

Discussion

There is increased interest in requiring circle hooks in the recreational bluewater troll fishery in the United States. This is largely due to studies finding that circle hooks maintain catch rates but reduce rates of deep hooking compared with J hooks in billfishes (see Serafy et al., 2009, for review). In contrast, we found for non-billfishes that observed catch rates were reduced with circle hooks under that for J hooks in the charter group; similar findings were found in the recreational group for dolphinfish. Predictions of relative catch (through effect

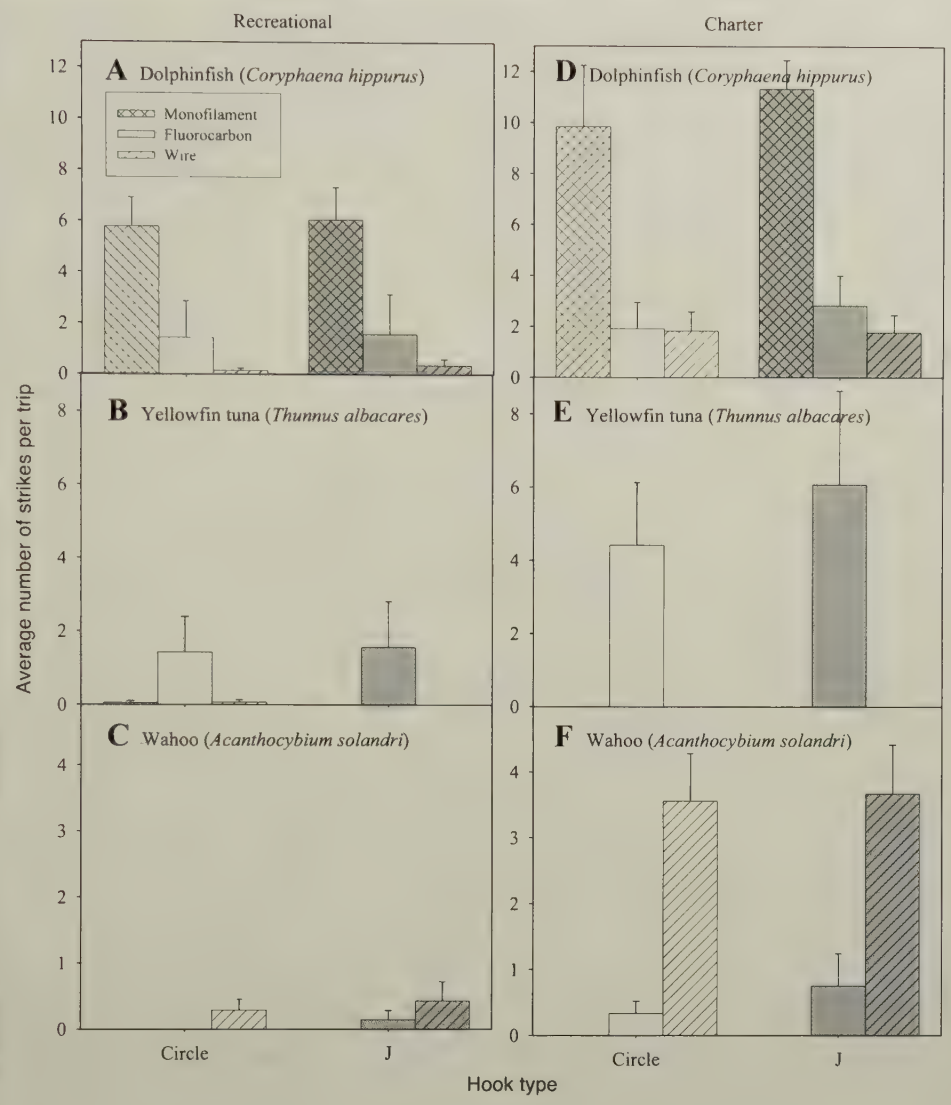

Figure 4

Plots of the average number of strikes per trip (±standard error) on circle hooks (open bars) and J hooks (gray bars). Data for plots includes strikes from unidentified fish later apportioned to species that could be identified. Data for each species are from both directed and nondirected trips for that species. Plots are broken down by user group (recreational [left column, panels **A–C**] and charter [right column, panels **D–F**]) and species (dolphinfish [*Coryphaena hippurus*] [A, D], yellowfin tuna [*Thunnus albacares*] [B, E], and wahoo [*Acanthocybium solandri*] [C, F]). The legend denoting fill pattern for each leader type applies to all panels. No bar for a particular hook-type+species+user-group+leader-type combination indicates no catch.

size calculations) indicate that fishermen can expect 65% greater catches of the three species or taxa groups on J hooks than on circle hooks. The similar findings between the species and taxa analyses indicate that morphological features of fish, attack styles, and hook effectiveness are consistent among the species of the tuna group and among the species of the mackerel group. Additionally, the similar results when smaller tunas and mackerels were included in the taxa analysis indicate that the ineffectiveness of circle hooks compared with J hooks is not size dependent within the range of fish sizes in our study.

The similarities between our findings and prior hook comparisons of hooks on longlines depend on the species being considered. In a Brazilian longline fishery, Sales et al. (2010) found a similar trend in dolphinfish catches to that found in our study (lower catches on circle hooks than on J hooks) but significantly more tunas caught on circle hooks than on J hooks. The increased catch

Table 3

Candidate models fitted to strike data for three species (dolphinfish [*Coryphaena hippurus*], yellowfin tuna [*Thunnus albacares*], and wahoo [*Acanthocybium solandri*]), and taxa (dolphinfish, tunas, and mackerels) when trolling circle and J hooks in Gulf Stream waters off North Carolina. Quasi-Akaike information criterion (QAIC) was used to evaluate model performance, with the lowest value indicating the most parsimonious model. Categorical predictor variables included hook type (hook), leader type (leader), species or taxa, and user group (user). Wave height was used as a continuous predictor variable. K=number of parameters for each model; w=Akaike weight. Base models included all predictor variables with exception of hook and any hook interactions; see *Methods* section for a full description of base models. ΔQAIC values ~<4 were considered models with reasonable support.

Interaction	Data type	Distribution	Model	K	QAIC	ΔQAIC	w
Strike: species	Count	Poisson	base + hook	15	979.96	0.00	0.36
			base	14	980.17	0.21	0.33
			base + hook + hook*user	16	981.89	1.93	0.14
			base + hook + hook*leader	17	983.42	3.46	0.06
			base + hook + hook*species	17	983.81	3.86	0.05
			base + hook + hook*user + hook*leader	18	985.40	5.44	0.02
			base + hook + hook*species + hook*user	18	985.75	5.79	0.02
			base + hook + hook*species + hook*leader	19	987.85	7.89	0.01
			base + hook + hook*species + hook*leader + hook*species*leader	23	996.39	16.43	0.00
B. Strike: taxa	Count	Poisson	base + hook	15	1050.57	0.00	0.40
			base	14	1051.09	0.52	0.31
			base + hook + hook*user	16	1052.66	2.08	0.14
			base + hook + hook*taxa	17	1054.54	3.97	0.05
			base + hook + hook*leader	17	1054.56	3.99	0.05
			base + hook + hook*taxa + hook*user	18	1056.59	6.01	0.02
			base + hook + hook*user + hook*leader	18	1056.64	6.07	0.02
			base + hook + hook*taxa + hook*leader	19	1058.92	8.34	0.01
			base + hook + hook*taxa + hook*leader + hook*taxa*leader	23	1067.40	16.83	0.00

rate of tunas on circle hooks over that for J hooks has been observed in other longline studies (Falterman and Graves, 2002). It is unclear what the mechanism is that leads to higher tuna catches on longline circle hooks, but lower tuna catches on trolled dead baits rigged with circle hooks; it is likely that tuna ingested the bait and hook more deeply in comparison to the actively trolled bait in our study. Actively trolling hooks (versus passive fishing on a longline) may be the mechanism contributing to these hook-type differences.

Most comparative studies of hooks in the dead bait troll fishery have been designed to estimate catch-and-release mortality in billfishes (Prince et al., 2002; Horodysky and Graves, 2005; Graves and Horodysky, 2010). The species that we examined in this study are not generally released; therefore, our focus was on the influence of hook type on catch rates and the potential mechanisms responsible for similarities or differences in catch by hook type, rather than on postrelease mortality. This was our focus because many charter boat captains suspect that circle hooks negatively impact catches of dolphinfish, tunas, and mackerels in the North Carolina dead-bait troll fishery. Our results confirm this suspicion. Model-averaged estimates suggest a strong negative effect of hook type on catch rates for all three species; however, examination of the raw data for individual species suggests that the effect of hook type on wahoo catch may be minor. Future studies with increased sample sizes would help to refine estimates of species by hook-type interactions, providing greater resolution of the importance and magnitude of hook effects for individual species. Thus, this is the first study to find that catch rates in a dead bait troll fishery can be negatively impacted by circle hooks. Horodysky and Graves (2005) and Graves and Horodysky (2010) did not provide comparisons of catch data between circle hooks and J hooks in their hook comparative studies on billfish.

Differences in strike, hook-up, and retention rates between hook types all have the potential to contribute to differences in catch rates. There was little evidence for a hook effect on strike rate; therefore, J and circle hook rigged baits were equally attractive to these three fish groups. Other studies that have compared hook types in the dead bait troll fishery have not reported data on strike rate by hook type; we recommend that this information be collected so that the specific mechanisms responsible for potential differences in catch rate can be determined.

The greater effectiveness of J hooks at hooking fish once they struck generally held across the three species and dolphinfish and the two taxa groups. Circle hooks

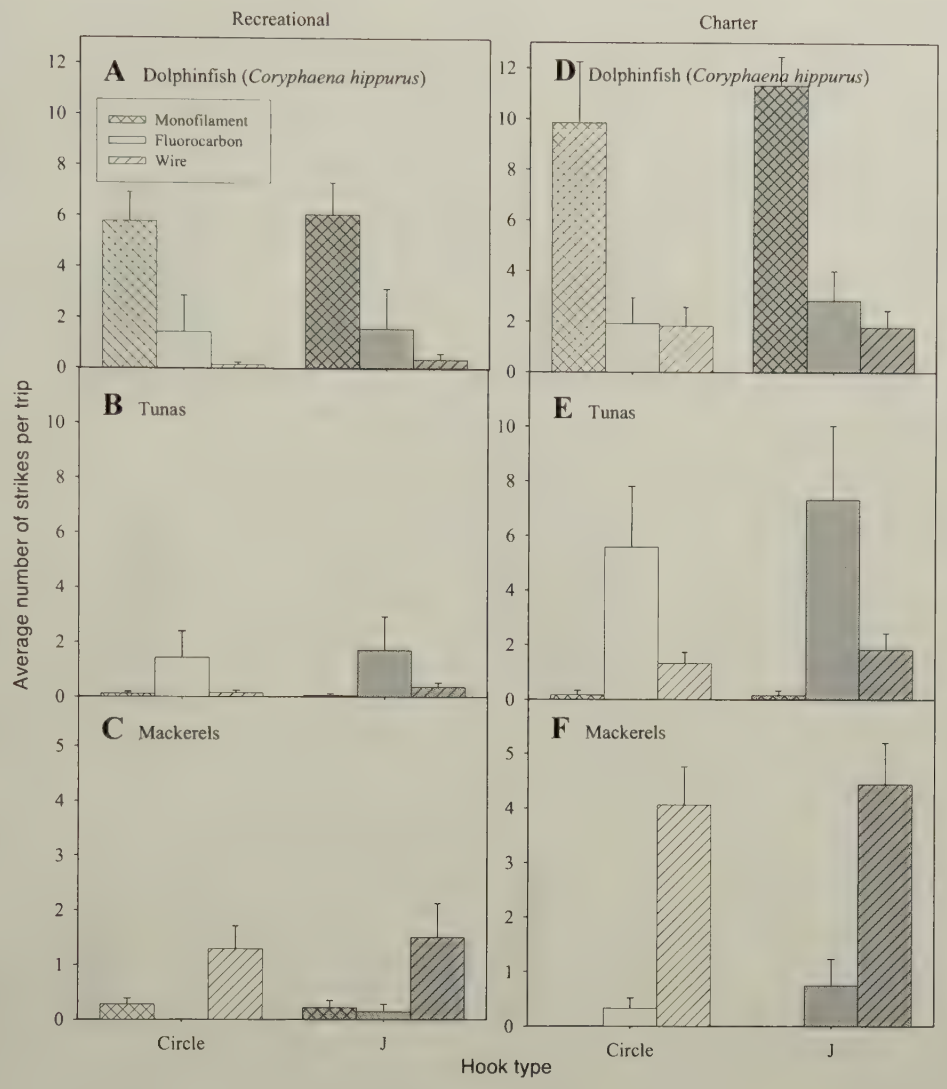

Figure 5

Plots of the average number of strikes per trip (±standard error) on circle hooks (open bars) and J hooks (gray bars). Data for plots include strikes from unidentified fish later apportioned to species that could be identified. Data for each group are from both directed and nondirected trips for that species. Plots are broken down by user group (recreational [left column, panels **A–C**] and charter [right column, panels **D–F**]) and taxa (dolphinfish [*Coryphaena hippurus*] [A, D], tunas [B, E], and mackerels [C, F]). The tuna group included yellowfin tuna (*Thunnus albacares*), blackfin tuna (*Thunnus atlanticus*), skipjack tuna (*Euthynnus pelamis*), and false albacore (*Euthynnus alletteratus*). The mackerel group included wahoo (*Acanthocybium solandri*), king mackerel (*Scomberomorus cavalla*), and Spanish mackerel (*Scomberomorus maculatus*). The legend denoting fill pattern for each leader type applies to all panels. No bar for a particular hook-type+taxon+user-group+leader-type combination indicates no catch.

are designed to hook fish if the hook rounds a corner within the jaw area. In theory, this would be most common for fish that turn their mouth opening away from the direction of the fishing line. However, if a fish is not seen during a strike, it is difficult to know when to reel the line tight (i.e., when the fish has turned). Our workshop panel (see *Methods* section) argued for a drop back for dolphinfish because this species is known to swim with the bait in their mouth in the direction that the line is trolled. The drop back for dolphinfish was done to allow enough time for the dolphinfish to turn. Even with these efforts, hook-up rates of dolphinfish were lower with circle hooks than J hooks for both user groups. Prince et al. (2002) found that hook-up

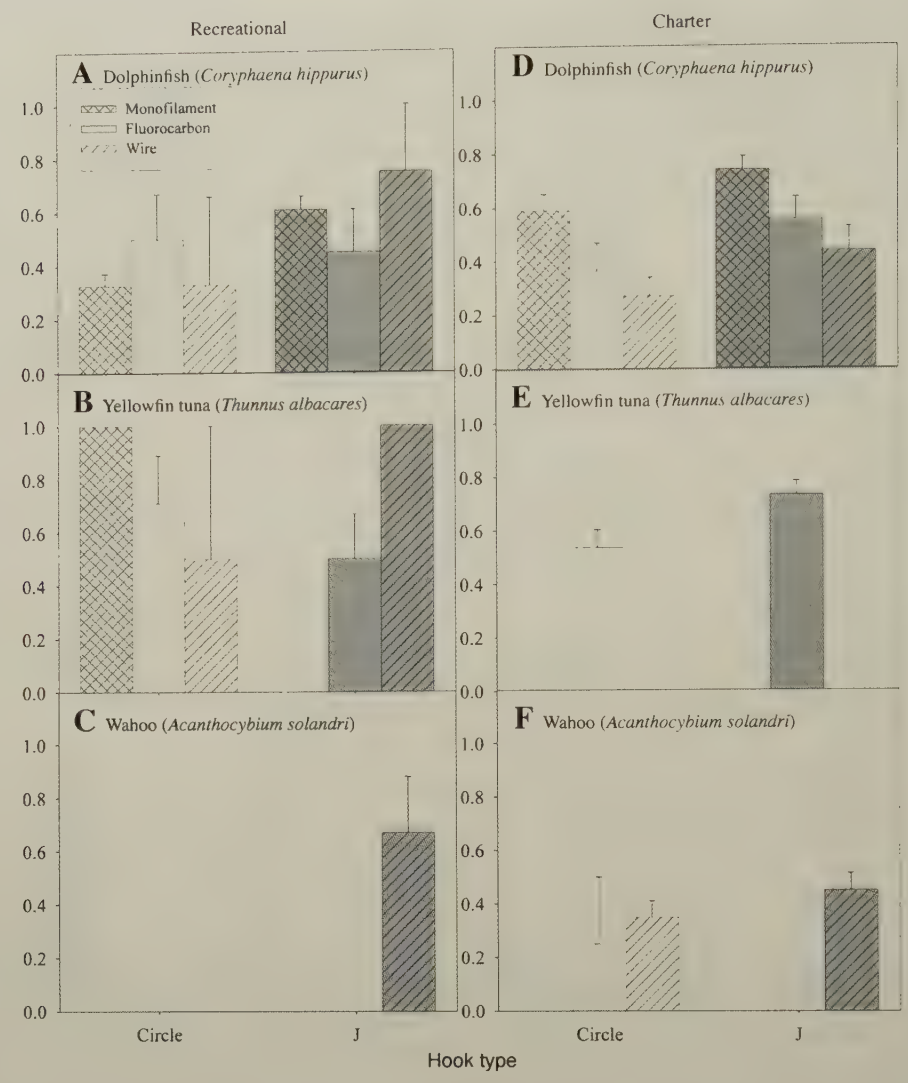

Figure 6

Plots of the average proportion of fish that hooked up (±standard error) on circle hooks (open bars) and J hooks (gray bars). Data for plots includes hook-ups from unidentified fish later apportioned to species that could be identified. Data for each species are from both directed and nondirected trips for that species. Plots are broken down by user group (recreational [left column, panels **A–C**] and charter [right column, panels **E–F**]) and species (dolphinfish [*Coryphaena hippurus*] [A, D], yellowfin tuna [*Thunnus albacares*] [B, E], and wahoo [*Acanthocybium solandri*] [C, F]). The legend denoting fill pattern for each leader type applies to all panels. No bar for a particular hook-type+species+user-group+leader-type combination indicates no catch.

rate on circle hooks was significantly higher than J hooks in a dead bait troll fishery for sailfish. The ability for the angler to visually see the fish with the bait in its mouth may allow for higher hook-ups on circle hooks in that fishery. In contrast, fishing for yellowfin tuna and wahoo involved using a heavy drag because the fish are aggressive and generally hook themselves upon striking (see Graves and Horodysky [2010] for a similar description and approach when targeting blue marlin). Theoretically, the circle hook should work in this heavy-drag situation only if the fish's mouth is at an angle to the direction of the line when the bait is taken into the mouth. Hook-up rates for yellowfin tuna and wahoo were slightly higher on J hooks on charter trips (for which we had the most data); this finding may be a result of some strikes on circle hooks where the mouth opening faced the direction that the bait was being trolled or because of bait rigging (see below). Graves

Table 4

Candidate models fitted to hook-up data for three species (dolphinfish [*Coryphaena hippurus*], yellowfin tuna [*Thunnus albacares*], and wahoo [*Acanthocybium solandri*]), and taxa (dolphinfish, tunas, and mackerels) when trolling circle and J hooks in Gulf Stream waters off North Carolina. Quasi-Akaike information criterion (QAIC) was used to evaluate model performance, with the lowest value indicating the most parsimonious model. Categorical predictor variables included hook type (hook), leader type (leader), species or taxa, and user group (user). Wave height was used as a continuous predictor variable. K=number of parameters for each model; w=Akaike weight. Base models included all predictor variables with exception of hook and any hook interactions; see *Methods* section for a full description of base models. ΔQAIC values ~<4 were considered models with reasonable support.

Interaction	Data type	Distribution	Model	K	QAIC	ΔQAIC	w
Hook-up: species	Proportion	Binomial	base + hook	11	−1159.03	0.00	0.38
			base + hook + hook*user	12	−1158.16	0.88	0.25
			base + hook + hook*species	13	−1156.75	2.29	0.12
			base + hook + hook*leader	13	−1156.53	2.51	0.11
			base + hook + hook*species + hook*user	14	−1155.07	3.96	0.05
			base + hook + hook*user + hook*leader	14	−1154.81	4.23	0.05
			base + hook + hook*species + hook*leader	15	−1154.75	4.28	0.04
			base + hook + hook*species + hook*leader + species*leader + hook*species*leader	23	−1148.53	10.51	0.00
			base	10	−1134.22	24.81	0.00
Hook–up: taxa	Proportion	Binomial	base + hook	11	−1393.91	0.00	0.40
			base + hook + hook*taxa	13	−1392.58	1.33	0.21
			base + hook + hook*user	12	−1392.17	1.74	0.17
			base + hook + hook*leader	13	−1390.90	3.00	0.09
			base + hook + hook*taxa + hook*user	14	−1390.48	3.43	0.07
			base + hook + hook*user + hook*leader	14	−1388.80	5.11	0.03
			base + hook + hook*taxa + hook*leader	15	−1388.72	5.19	0.03
			base + hook + hook*taxa + hook*leader + taxa*leader + hook*taxa*leader	23	−1385.27	8.64	0.01
			base	10	−1368.17	25.74	0.00

and Horodysky (2010) did not report hook-up percentage data for blue marlin and therefore it is unknown what hook-up rates would be for this aggressive feeder that is hooked upon strike.

One rigging tactic when trolling is to rig the circle hook so that it is completely external to the bony or fleshy portions of the bait to maximize the exposed gap width (e.g., the hook is placed on top of the bait's head; Prince et al., 2002). This placement is thought to work best for "dropping back" to fish because the fish have enough time to swallow the bait and the hook (dolphinfish and billfish trolling) and turn their body, while the exposed gap width of the circle hook is maximized. We did not employ the external rigging technique on days when yellowfin tuna or wahoo were targeted. Hooks were rigged internally for these two species because these species hook themselves upon striking; drop-backs are not typically required by charter or recreational fishers targeting these species. An additional reason for embedding hooks in baits was so that we could fish "combo" baits (lure and natural bait combinations) because colored lures (skirts) elicit more strikes than plain ballyhoo on most days for yellowfin tuna and wahoo. The cooperating mates on charter trips embedded the hook as close to the tail as possible without compromising the swimming action of the bait. Using larger circle hooks would have increased the gap width between the point and the point shank, potentially making hook-ups more likely, but this change could have compromised the strike rate by making the hook more visible to the fish or causing the bait to wash out faster.

There was little to no hook effect at the proportional retention level (caught once hooked) for dolphinfish, yellowfin tuna, and tunas, although there was increased retention of wahoo and mackerels on circle hooks and yellowfin tuna on circle hooks in the recreational fishery. The latter result is consistent with the findings of Prince et al. (2002) when trolling dead baits with circle and J hooks for sailfish. The increased retention on circle hooks relative to J hooks has been used as a selling point for circle hooks, but we did not find this result for the majority of species that we caught.

The procedure for assigning interactions with unidentified fish to a particular species is not ideal. For instance, if individuals of one species generate behavioral cues or are landed more readily than individuals for another species, species assignments may be biased toward more readily identified fish. In general, this approach decreased our ability to detect species effects on landing probabilities and hookup rates. However, we expected the reduction in statistical power to be relatively small and to affect only inferences about

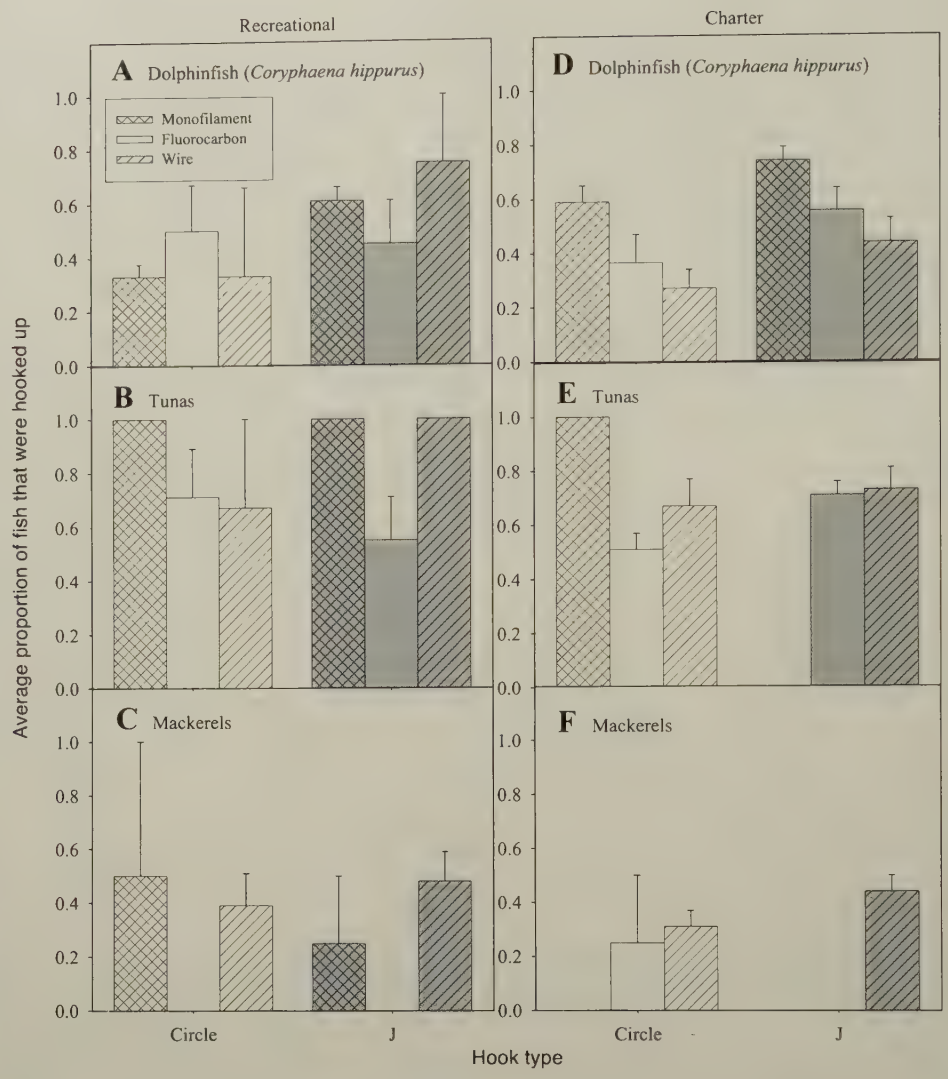

Figure 7

Plots of the average proportion of fish that hooked up (±standard error) on circle hooks (open bars) and J hooks (gray bars). Data for plots includes hook-ups from unidentified fish later apportioned to species that could be identified. Data for each group are from both directed and nondirected trips for that species. Plots are broken down by user group (recreational [left column, panels **A–C**] and charter [right column, panels **E–F**]) and taxa (dolphinfish [*Coryphaena hippurus*] [A, D], tunas [B, E], and mackerels [C, F]). The tuna group included yellowfin tuna (*Thunnus albacares*), blackfin tuna (*Thunnus atlanticus*), skipjack tuna (*Euthynnus pelamis*), and false albacore (*Euthynnus alletteratus*). The mackerel group included wahoo (*Acanthocybium solandri*), king mackerel (*Scomberomorus cavalla*), and Spanish mackerel (*Scomberomorus maculatus*). The legend denoting fill pattern for each leader type applies to all panels. No bar for a particular hook-type+taxon+user-group+leader-type combination indicates no catch.

species-hook interactions; main effects for hook type remained unbiased.

If fishermen are interested in releasing dolphinfish, our results provide evidence that released fish are not hooked as deeply and thus have a higher likelihood of survival if circle hooks are used. The drop-back technique that we commonly used for dolphinfish likely led to a higher percentage of dolphinfish becoming deep hooked with J hooks over that for the tuna and mackerel taxa groups. The reduction in gut hooking with circle hooks has been found in most other studies comparing circle and J hooks (Cooke and Suski, 2004). Managers should factor in the high rate of deep hooking for J-hooked dolphinfish as they imple-

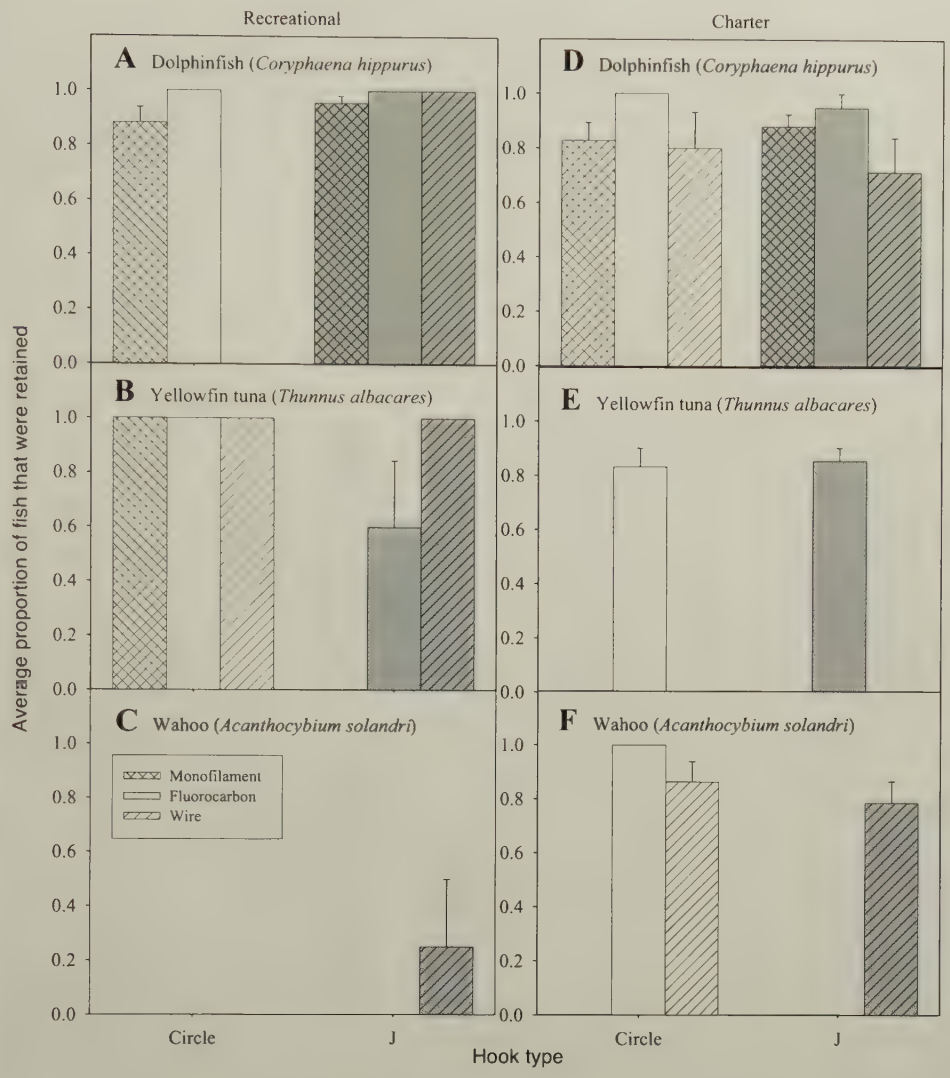

Figure 8

Plots of the average proportion of fish retained (±standard error) on circle hooks (open bars) and J hooks (gray bars). Data for each species are from both directed and non-directed trips for that species. Plots are broken down by user group (recreational [left column, panels **A–C**] and charter [right column, panels **D–F**]) and species (dolphinfish *Coryphaena hippurus* [A, D], yellowfin tuna [*Thunnus albacares*] [B, E], and wahoo [*Acanthocybium solandri*] [C, F]). The legend denoting fill pattern for each leader type applies to all panels. No bar for a particular hook-type+species+user-group+leader-type combination indicates no catch.

ment new minimum size regulations for this species in the U.S. South Atlantic (SAFMC, 2011). However, managers should also consider that there can be a trade-off when using circle hooks. Although rates of deep hooking are relatively low on circle hooks, handling time and air exposure are increased while dislodging them from captured fish owing to their inherently deeper bend than J hooks (Cooke and Suski, 2004; senior author, personal observ.). Along with outreach efforts to encourage the use of circle hooks where appropriate, instructions should be available on how to quickly remove the hooks with little injury to the fish.

Circle hooks remain vaguely defined. The federal definition of a circle hook (Federal Register, 2006) is somewhat arbitrary. Numerous circle hooks may meet the federal specifications, yet may not simultaneously reduce deep hooking in billfishes and maintain catch rates of non-billfishes. For example, some manufacturers advertise circle hooks with parallel or nearly parallel point shanks and hook shanks (like a J hook), but which simply have the tip of the point bent 90°

Table 5

Candidate models fitted to retention data for three species (dolphinfish [*Coryphaena hippurus*], yellowfin tuna [*Thunnus albacares*], and wahoo [*Acanthocybium solandri*]), and taxa (dolphinfish, tunas, and mackerels) when trolling circle and J hooks in Gulf Stream waters off North Carolina. Quasi-Akaike information criterion (QAIC) was used to evaluate model performance, with the lowest value indicating the most parsimonious model. Categorical predictor variables included hook type (hook), leader type (leader), species or taxa, and user group (user). Wave height was used as a continuous predictor variable. K=number of parameters for each model; w=Akaike weight. Base models included all predictor variables with exception of hook and any hook interactions; see *Methods* section for a full description of base models. ΔQAIC values ~<4 were considered models with reasonable support.

Interaction	Data type	Distribution	Model	K	QAIC	ΔQAIC	w
Retention: species	Proportion	Binomial	base	10	−876.22	0.00	0.63
			base + hook	11	−874.19	2.02	0.23
			base + hook + hook*leader	13	−871.13	5.09	0.05
			base + hook + hook*species	13	−870.76	5.46	0.04
			base + hook + hook*species + hook*user	14	−869.35	6.87	0.02
			base + hook + hook*user + hook*leader	14	−869.16	7.05	0.02
			base + hook + hook*species + hook*leader	15	−867.10	9.12	0.01
			base + hook + hook*user	12	−857.77	18.45	0.00
			base + hook + hook*species + hook*leader + species + leader hook*species*leader	23	−854.71	21.51	0.00
Retention: Taxa	Proportion	Binomial	base	12	−1112.66	0.00	0.53
			base + hook	13	−1110.55	2.11	0.19
			base + hook + hook*species	15	−1108.74	3.92	0.08
			base + hook + hook*user	14	−1108.74	3.93	0.08
			base + hook + hook*leader	15	−1108.54	4.12	0.07
			base + hook + hook*species + hook*user	16	−1106.71	5.95	0.03
			base + hook + hook*user + hook*leader	16	−1106.40	6.26	0.02
			base + hook + hook*species + hook*leader	17	−1104.87	7.79	0.01
			base + hook + hook*species + hook*leader + hook*species*leader	23	−1092.10	20.56	0.00

Table 6

Percentage of fish caught in two anatomical locations (jaw vs. "deep" [body, gill, gut, eye]) with trolled circle and J hooks. The χ^2 test statistic and P-value from each test of independence comparing hooking locations between hook types are presented for each species. A χ^2 test was not conducted for king mackerel because of small sample size.

	Circle hook		J hook			
Species	Jaw	Deep	Jaw	Deep	χ^2	P
Dolphinfish (*Coryphaena hippurus*)	98.5	1.5	61.3	38.7	31.35	<0.001
Yellowfin tuna (*Thunnus albacares*)	100	0	100	0	—	—
Wahoo (*Acanthocybium solandri*)	100	0	91.3	8.7	1.82	0.177
Blackfin tuna (*Thunnus atlanticus*)	100	0	92.6	7.4	1.13	0.287
King mackerel (*Scomberomorus cavalla*)	100	0	66.7	33.3		

toward the shank. Having discussed the structure of the hooks with captains, Smith (2006) postulated that a greater turn in the point shank (a point shank that turns back towards the hook shank by ≥33°) reduces the chances for deep hooking in billfishes. This outcome has yet to be determined with experimental fishing and would be a useful area of future research. We measured the angle between the point shank and hook shank to be roughly 25 degrees for the circle hooks we used (regardless of the size). Compared with the circle hook styles we tested, other circle hooks with different point shank angles that still satisfy federal requirements may have performed better at catching non-billfish species.

The fishing tackle industry and charter boat operators continually adapt gear and techniques to increase

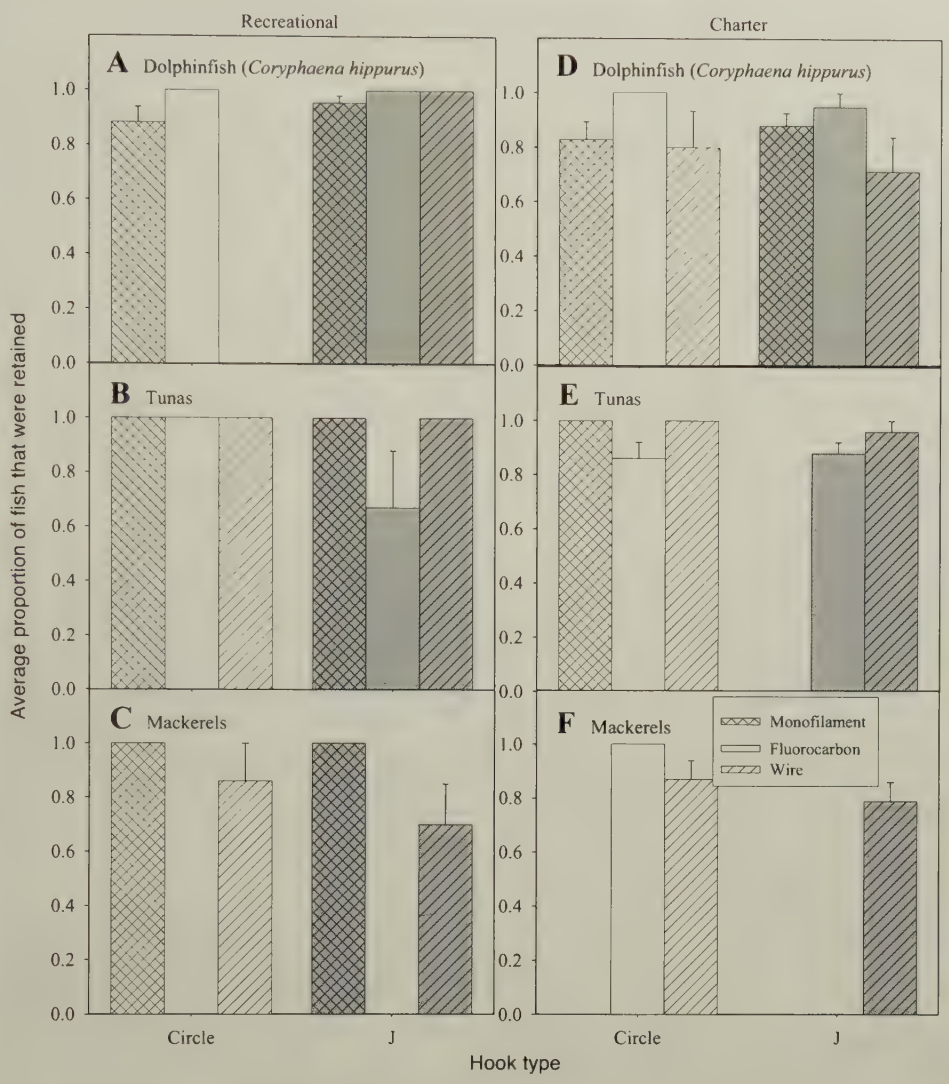

Figure 9

Plots of the average proportion of fish retained (±standard error) on circle hooks (open bars) and J hooks (gray bars). Data for each group are from both directed and nondirected trips for that species. Plots are broken down by user group (recreational [left column, panels **A–C**] and charter [right column, panels **D–F**]) and taxa (dolphinfish *Coryphaena hippurus* [A, D], tunas [B, E], and mackerels [C, F]). The tuna group included yellowfin tuna (*Thunnus albacares*), blackfin tuna (*Thunnus atlanticus*), skipjack tuna (*Euthynnus pelamis*), and false albacore (*Euthynnus alletteratus*). The mackerel group included wahoo (*Acanthocybium solandri*), king mackerel (*Scomberomorus cavalla*), and Spanish mackerel (*Scomberomorus maculatus*). The legend denoting fill pattern for each leader type applies to all panels. No bar for a particular hook-type+taxon+user-group+leader-type combination indicates no catch.

catch efficiency. There are likely untested techniques that allow fishermen to catch non-billfish with circle hooks more efficiently than we found in this study. Cooke and Suski (2004) report that the choice of circle hook size is an important consideration in order to maximize their effectiveness. Hook size seems to be an especially important consideration in a mixed-species and mixed-size fishery such as the one we examined. Hook choice (size and style) was a central topic in the workshop we convened; in targeting each of the main species (dolphinfish, yellowfin tuna, and wahoo), we selected hook sizes and styles recommended by experienced offshore fishermen.

It is likely that fishermen would be more inclined to experiment with circle hooks and novel rigging strategies if they knew there would be a pending re-

quirement to use them outside of Atlantic billfish tournaments. Industry willingness to refine rigging techniques and fishing strategies in the face of future hook-type regulations could help increase experimentation with circle hooks, and thus catch rates of non-billfish species when trolling for them in this fishery. The workshop we convened generated many novel rigging and fishing techniques with circle hooks, only a fraction of which we used for the field experiment of this project.

We urge future studies to provide catch rates (numbers standardized to effort), strike, hook-up, and retention data for both hook types so that trade-offs between catch-and-release survival and catch rates can be evaluated. In addition, the terms used when discussing these variables should also be standardized. For example, the catch rate for trolled baits as defined by Serafy et al. (2009) equals a retention rate (caught if hooked), but a fisherman's interest lies in knowing how many fish will be caught per trip which is the product of number of strikes, proportion hooked, and proportion retained. Without knowledge of the first two variables, the third variable only provides information about a hook's effectiveness at retaining a fish on the line and not its overall effectiveness.

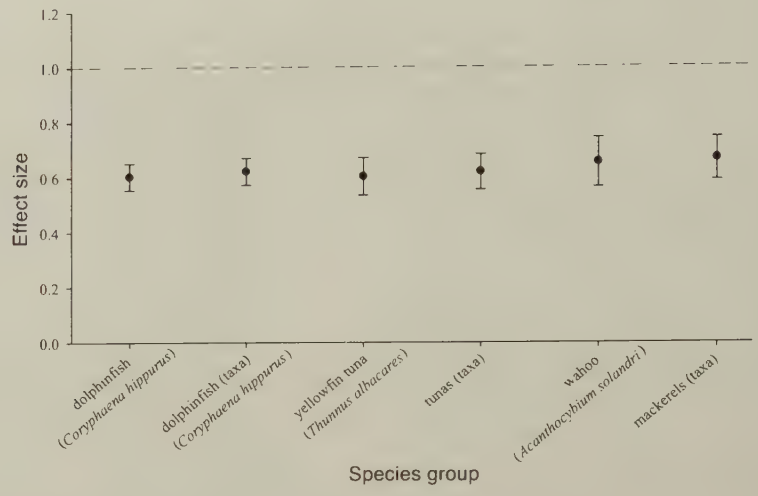

Figure 10

Mean predicted effect size (±standard deviation) of circle versus J hooks on catch rates by species or taxa group. Dolphinfish (*Coryphaena hippurus*) is listed twice because the predicted effect size changes slightly in comparisons with the "tunas" and "mackerels" taxa groups. An effect size greater than 1 indicates greater effectiveness of circle hooks than J hooks; the opposite is true for an effect size less than 1. An effect size equal to 1 (dashed line) indicates that the hook types are equally effective. The mean and variance of each effect size was calculated by using weighted model averages from each model with positive Akaike weight (w_i) at the catch level (see *Materials* section for details).

Conclusions

We examined three mechanisms that may have been responsible for the hook effect on catch rates. These were strike, hook-up, and retention. There was little to no hook effect at the strike and retention levels. However, the differences in catch rates we observed resulted from a lower hook-up rate on circle hooks compared with J hooks. This trend was generally consistent across analyses of data on three species and on three broader taxa.

It is unknown whether a requirement to troll exclusively circle hooks in the offshore fishery would have an economic impact on either the recreational or charter fisheries in this region. It is likely that circle hooks need to catch fish at rates near, equal to, or higher than J hooks to gain wider acceptance among offshore troll fishermen (Jordan, 1999). We hope that angler experimentation will lead to improvements in circle hook catch rates for non-billfish species caught during trolling operations.

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Distribution, movements, and habitat use of small striped bass (*Morone saxatilis*) across multiple spatial scales

Kenneth W. Able[1]
Thomas M. Grothues[1]
Jason T. Turnure[1]
Donald M. Byrne[2*]
Paul Clerkin[1]

E-mail address for contact author: able@marine.rutgers.edu

[1] Rutgers University Marine Field Station
800 c/o 132 Great Bay Blvd.
Tuckerton, New Jersey 08087

[2] New Jersey Department of Environmental Protection
Nacote Creek Research Station
P.O. Box 418
Port Republic, New Jersey 08241

* Posthumous

Abstract—Distribution, movements, and habitat use of small (<46 cm, juveniles and individuals of unknown maturity) striped bass (*Morone saxatilis*) were investigated with multiple techniques and at multiple spatial scales (surveys and tag-recapture in the estuary and ocean, and telemetry in the estuary) over multiple years to determine the frequency and duration of use of non-natal estuaries. These unique comparisons suggest, at least in New Jersey, that smaller individuals (<20 cm) may disperse from natal estuaries and arrive in non-natal estuaries early in life and take up residence for several years. During this period of estuarine residence, individuals spend all seasons primarily in the low salinity portions of the estuary. At larger sizes, they then leave these non-natal estuaries to begin coastal migrations with those individuals from nurseries in natal estuaries. These composite observations of frequency and duration of habitat use indicate that non-natal estuaries may provide important habitat for a portion of the striped bass population.

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A full understanding of the distribution, movements, and habitat use of juvenile and other subadult striped bass (*Morone saxatilis*) is central to deciphering the role, impacts, and management of this abundant and important species in estuarine and coastal ocean habitats. This is especially true for the populations between Chesapeake Bay and the Gulf of Maine where adults can be highly migratory and are seasonal participants in coastal migrations (Chapoton and Sykes, 1961; Boreman and Lewis, 1987; Waldman et al., 1990; Able and Grothues, 2007; Welsh et al., 2007; Grothues et al., 2009; Mather et al., 2010). More recently, it has become apparent that some components of these same populations may be resident in estuaries throughout their life cycle (Secor, 1999; Secor and Piccoli, 2007; Wingate and Secor, 2007). Despite the accumulating understanding of life cycle diversity for adults (see Secor and Kerr, 2009 for *M. saxatilis* and other species), we have an incomplete understanding for juveniles and other subadults (Pautzke et al., 2010). The conventional interpretation based on studies of natal estuaries, including Chesapeake Bay and other large estuaries (Merriman, 1941; Mansueti, 1961; Waldman et al., 1990), is that juveniles remain in estuaries for the first few years of life before leaving to join the coastal migration and may stay longer, if they are natal estuarine residents (Secor 1999; Ashley et al., 2000; Secor and Piccoli, 2007).

For those individuals that eventually become coastal migrants, the available data suggest that the duration of residency in estuaries appears to vary with location and between years, potentially relative to year class strength and associated density dependence (e.g., Kohlenstein, 1981), as well as size and maturity for males and females (e.g., Kohlenstein, 1981; Secor and Piccoli, 2007). For example, an early interpretation was that a mass emigration of small individuals takes place from Chesapeake Bay after ages 2 and 3 (Kohlenstein, 1981). More recently, analysis with otolith microchemistry suggests a gradual shift associated with sexual maturation at ages 5–8 for upper Chesapeake Bay individuals (Secor and Piccoli, 2007). In the Hudson River, it is estimated that emigration from the estuary can occur into adjacent Long Island Sound and the New York Bight at ages 1 and 2 (Secor and Piccoli, 1996) or earlier by age-0 individuals (Dovel 1992, Dunning et al., 2009).

Our understanding of the distribution, movements, and habitat use of small striped bass is largely based on studies that occurred before the recovery in the late 1980s (Nichols and Miller, 1967; Clark, 1968; Kohlenstein, 1981; Boreman and Lewis, 1987; Wooley et al., 1990; Richards and Rago, 1999). Further, most studies have focused on large natal estuaries such as the Hudson River (Secor and Piccoli, 1996), Chesapeake Bay (Mansueti, 1961; Kohlenstein, 1981; Secor, 2007), and to some extent the Delaware River (Waldman and Wirgin, 1994; Able et al., 2007). There has been little emphasis on non-natal estuaries even though small striped bass are common and even abundant components of the fauna (for reviews see Able and Fahay, 1998, 2010). Therefore, we lack a clear understanding of their pattern of habitat use within estuaries, duration of residency, and patterns of timing of emigration (Grothues et al., 2009). These patterns are especially confounded because the sources of small individuals in non-natal estuaries are largely unknown.

The purpose of this article is to evaluate the distribution, movements, and habitat use of small striped bass in and adjacent to non-natal estuaries in New Jersey and adjacent areas. We approach this evaluation using multiple sources including information from seasonal catches from trawl, seine, and gill net surveys, tag-recapture studies, and telemetry. Most of these data relate to a period during or after the recovery of the population along the east coast. Further, we evaluate these patterns of estuarine and coastal ocean use at three scales: throughout the Middle Atlantic Bight continental shelf (Cape Cod to Cape Hatteras); on the inner continental shelf off New Jersey; and in the Mullica River–Great Bay estuary in southern New Jersey. Although the focus is on small individuals, i.e., from young-of-the-year to sexual maturity, the duration of this stage is sometimes difficult to define because the age (and size) at maturity varies between sexes, populations, and even within the same estuary (see Fig. 1 in Specker et al., 1987). We define the upper size limit for our treatment as 46 cm total length (TL) (approx. age 3–5 years; Merriman, 1941). In addition, there appears to be a natural difference in the size modes of several extensive sampling programs around this size (see below). The rationale for using this cutoff is that it includes the size at first maturity for some populations and that it complements our earlier telemetry studies of larger striped bass in the Mullica River–Great Bay estuary (Able and Grothues, 2007; Ng et al., 2007; Grothues et al., 2009). Thus, those individuals <46 cm include those likely to be resident in estuaries, such as mature males (e.g., Wingate and Secor, 2007), but also include those that may begin leaving estuaries to participate in coastal migrations. For the purposes of this article, we make a distinction, where possible, between dispersal (from natal estuaries) by juveniles (<20 cm) and other individuals of unknown maturity (>20–46 cm) and dispersal by those that make (directed, annual) coastal migrations.

Materials and methods

Study areas

We used three geographical areas in this study (Fig. 1): 1) continental shelf waters (to depths greater than 450 m) along the east coast of the United States between Cape Hatteras and Cape Cod; 2) a portion of the inner continental shelf (depths of 5.5–27.4 m) off the coast of New Jersey; and 3) the Mullica River–Great Bay estuary (average depth 2 m, some portions to 26 m) which is part of the Jacques Cousteau National Estuarine Research Reserve (JCNERR). Aspects of the geomorphology and hydrology of each of these areas is characterized in further detail elsewhere (Able and Fahay, 1998; 2010).

Occurrence and distribution based on surveys

Seasonal, coast-wide distributions for small (<46 cm) striped bass on the continental shelf were determined with data from National Marine Fisheries Service (NMFS) Northeast Fisheries Science Center bottom trawl surveys (Azarovitz, 1981; Grosslein and Azarovitz, 1982) (Fig. 1, Table 1). Samples were collected on the continental shelf at stratified random stations between Cape Hatteras, North Carolina, and the Gulf of Maine during fall (September–October), winter (January–February) and spring (March–April) (Grosslein and Azarovitz, 1982; Able and Fahay, 2010). The geographical limits of the sampling program, however, varied with season and between years. Similar sampling effort and distribution of samples occurred in the fall (n=7379 tows) and spring (n=7418 tows) over the period from 1982 through 2003. The winter sampling effort was reduced in terms of number of tows (n=1552 tows) and geographical extent during the years in which it occurred (1992–2003). It was limited to the southern portion of Georges Bank and south of Cape Cod to just north of Cape Hatteras. In addition, the number of samples in the shallow waters (less than 25 m) off Massachusetts and from New Jersey to North Carolina was reduced in the winter but not in the fall and spring. The distribution of samples over all seasons varied with depth as well, with some less than 20 m (17%), a large portion less than 100 m (81%), fewer between 100 and 250 m (16%) and fewer still in depths >251 m (2%). See Able and Fahay (2010) for additional details. An estimate of the length distribution by age of striped bass was based on data from Mansueti (1941) and Able and Fahay (1998) and back-calculated length at age was based on otoliths of striped bass collected in Delaware Bay by the New Jersey Department of Environmental Protection (Baum[1]).

Distribution data for small (<46 cm) striped bass off New Jersey were collected seasonally by otter trawl from 1996 to 2003 by randomly selecting sites in each of 15 sampling strata by the New Jersey Department

[1] Baum, T. 2006. Personal commun. New Jersey Dep. Environmental Protection, Nacote Creek Research Center, Port Republic, NJ 08241.

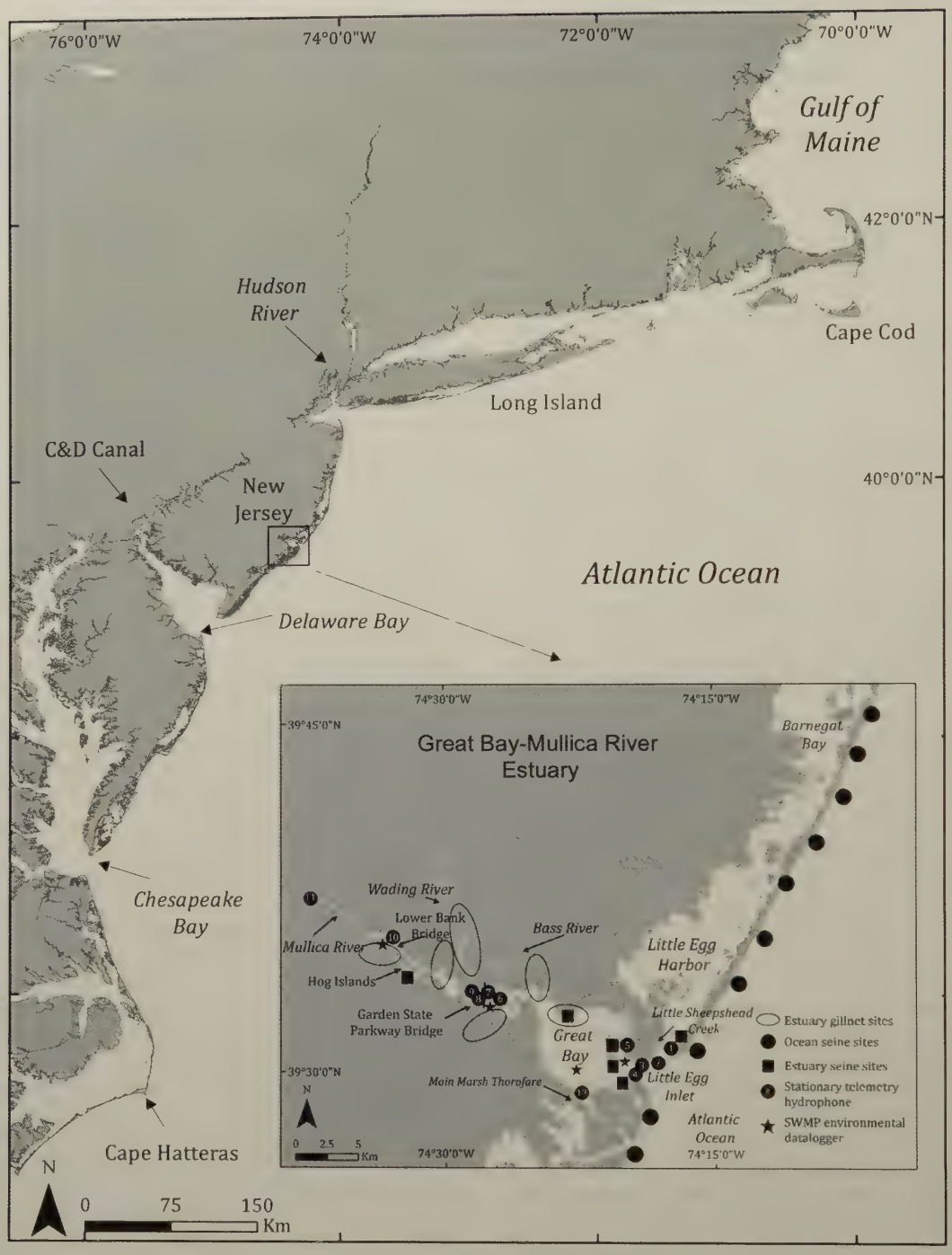

Figure 1

Collection sites for striped bass (*Morone saxatilis*) within the Mid-Atlantic Bight. Striped bass were collected by the National Marine Fisheries Service's otter trawl survey (between Cape Cod and Cape Hatteras), New Jersey Department of Environmental Protection's otter trawl survey (coast of New Jersey), and Rutgers University Marine Field Station's estuarine-ocean beach-seine and estuarine gillnet surveys. Stationary telemetry hydrophone and water quality data logger locations (in the vicinity of Little Egg Inlet and the Mullica River–Great Bay estuary [inset]) are also shown. See Table 1 for timing of sampling.

of Environmental Protection (NJDEP) (Fig. 1, Table 1). See Byrne[2] and Sackett et al. (2007) for additional details. These sites were divided into three depth strata and categorized as inshore (5.5–9.1 m), mid-shore

[2] Byrne, D. M. 1989. New Jersey trawl surveys. *In* Special Report No. 17 of the Atlantic States Marine Fisheries Commission (Azarovitz, T. R., J. McGurrin, and R. Seagraves, eds.), p. 46–48. Atl. States, Marine Fish. Comm.,Woods Hole, MA.

(9.1–18.3 m), and offshore (18.3–27.4 m). Trawl locations were mapped with GIS (ArcGIS[3], vers. 9.2, ESRI, Redlands, CA). The entire otter trawl data matrix consisted of 2872 records of catch per unit of effort (CPUE; number of individuals per tow), average depth, date, season (spring, April; summer, June–August; fall, September–October; winter, January–February), and depth category (inshore, midshore, and offshore). Additional collections from the surf zone adjacent to and within the Mullica River–Great Bay estuary were collected by seine during 1998–99 and 2004–06 (Table 1, Fig. 1). See Taylor et al. (2007) for additional details.

In order to determine the estuarine distribution of other small (<46 cm) striped bass in space and time, we sampled with anchored multimesh gill nets (15 m×2.4 m nets with five panels of five box-mesh sizes 2.5, 3.8, 5.1, 6.4, and 7.6 cm) in the Mullica River–Great Bay estuary at several locations (Table 1, Fig. 1). Gill nets were set (for approximately 60 min during the day) at biweekly intervals during the spring, summer, and fall in upper creek, creek mouth, and nearshore bay habitats. Within each area, the position in which each net was set varied such that no two locations were sampled twice. See Able and Fahay (2010) for additional details.

Another sampling program was conducted with small otter trawls between 1988–90 and 1996–2009 at a variety of stations and habitats located throughout the Mullica River–Great Bay–Inner Continental Shelf corridor (Table 1). These stations were distributed along the salinity gradient from the ocean to tidal freshwater. Other individuals were collected in composite surveys in Delaware Bay with a variety of gear types and from habitats during 1998–2006 (Table 1; Able et al., 2007; Able and Fahay, 2010). Still others came from an extensive seine survey in the Hudson River estuary (Table 1).

Tag-recapture

The tagging procedure outlined in Boreman and Lewis (1987) for their study with American Littoral Society (ALS) data is consistent with the protocol followed in our study. After initial capture, code-specific loop tags were inserted into the dorsal region of each fish and the fish was released. Length, general capture and release location, and date were recorded for each animal on a supplied tagging card and mailed to ALS. The ALS sends raw data to the National Marine Fisheries Service in Woods Hole, Massachusetts, for processing and entry into a long-term database (Shepherd[4]). We limited the query of records to two subsets of data: 1) striped bass initially captured in New Jersey waters and recaptured at less than 46 cm TL along the eastern United States coast; and 2) striped bass initially captured in nearby natal estuaries (Hudson and Delaware rivers) and recaptured in New Jersey waters at less than 46 cm TL (Table 1). The latitude and longitude coordinates associated with each general capture and recapture location were assigned by ALS and NMFS by calculating the spatial average of each location submitted by volunteer taggers.

Telemetry

We determined dynamic habitat use and movements of small (32.4–42.5 cm fork length [FL]) striped bass in the Mullica River–Great Bay estuary using acoustic telemetry. Wireless hydrophones were moored as a series of gates in order to determine occurrence and residency of tagged individuals along the estuarine gradient (Fig. 1). Fishes surgically implanted with individually coded acoustic transmitters (76.8 kHz) were detected when they came within range (approximately 500 m) of moored wireless hydrophones (WHS-1100, Lotek Wireless, Inc., St. Johns, Newfoundland, Canada) suspended at a depth of approximately 3.2 m (see Grothues et al. [2005] for additional details). Permanent environmental-monitoring instruments in the Jacques Cousteau National Estuarine Research Reserve included data loggers recording salinity, temperature, pH, and water depth (Kennish and O'Donnell, 2002) along the estuarine gradient (Fig. 1).

In addition, mobile tracking methods were used to determine fine-scale patterns of habitat use. In order to spatially and temporally standardize tracking, 113–120 fixed locations were georeferenced with a global positioning system (GPS) unit in universal transverse mercator (UTM) coordinates by using a GIS software package (ArcGIS, vers. 9.2, ESRI) and visited with a directional mobile hydrophone on a weekly basis (LHP_1; Lotek Wireless). Listening range with the mobile hydrophone was typically about 500 m, determined by signal range tests. At each of the above locations, the hydrophone was lowered 1.0 m into the water and pointed at the four principal ordinates for 5 seconds in each direction. When a fish was detected, its position was triangulated by moving until a reading of 115 dB or above was detected at a gain of 15 or less (approximately 2 m from the hydrophone). Measurements of water temperature and salinity were collected (YSI Model 85; Yellow Springs Instruments, Inc., Yellow Springs, Ohio), along with date, time, tag number, and depth at each confirmed fish detection. Tracking was not conducted when the listening range was less than 500 m (which corresponded to wind velocities greater than 30 km/h) or on days when there was heavy rainfall or thunderstorms. See Ng et al. (2007) and Sackett et al. (2008) for further details on mobile tracking protocol. To determine patterns of seasonal habitat use in relation to physical habitat variables, the distances of individually tagged striped bass from emergent (marsh) and submerged (channel) embankment edges were calculated by using a GIS software package. The locations of submerged edges were derived from estuarine bathymetry data by calculating high slope areas (i.e., channel edges; >2.5°) and submerged or emergent edge

[3] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

[4] Sheperd, G. 2009. Personal commun. NMFS Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA 02543-1026.

Table 1

Summary of data sources for juvenile striped bass (*Morone saxatilis*) examined in the current study. See Fig. 1 for sampling locations.

General habitat	Geographic location	Sampling gear	Sampling frequency/duration
Ocean	Atlantic coast	Otter trawl	Fall, winter, spring/1982–2003
	Atlantic coast	Tag-recapture	Fall, winter, spring, summer/1962, 1967, 1973, 1977–2009
	New Jersey coast	Otter trawl	Fall, winter, spring, summer/1988–2003
	Central New Jersey coast	Seine	Biweekly/June – November 1998, May–October 1999–2000, July 2004, May–October 2005, August–October 2006
Estuary	Mullica River-Great Bay	Otter trawl	Monthly/July and September 1988–1990, 1996–2009
	Mullica River-Great Bay	Multi-mesh gill net	Monthly/August–October 2001; Semi-monthly/May–October 2002
	Mullica River- Great Bay	Seine	Biweekly/June – November 1998, May–October 1999–2000, July 2004, May–October 2005, August–October 2006
	Mullica River-Great Bay	Acoustic telemetry	Mobile (Weekly/2006–2008) Passive (Continuous/2006–2008)
	Delaware Bay	Otter trawl/weirs	Monthly/April – November 1996–2000; May–November 2001–2005
	Hudson River	Seine	July–November 1990–2009

distances were calculated as the straight-line distance (m) to the nearest edge.

Results

Occurrence and distribution based on surveys

Small (<46 cm TL) striped bass were represented in multiple sampling gears from multiple locations throughout the study area (Table 1, Fig. 2). However, individuals <20 cm (presumed age 0–1 years) were seldom collected in the coastal ocean, including the NMFS trawl survey between Cape Hatteras and Cape Cod (n=2 individuals), the NJDEP trawl survey (n=61 individuals), and the Rutgers University Marine Field Station (RUMFS) beach seine survey along the inner continental shelf off New Jersey (n=21 individuals) despite the large number of samples. These smaller individuals were also not abundant in estuarine seine, gill net, or otter trawl collections within the Mullica River–Great Bay estuary based on over 3100 samples (Table 1, Fig. 2). Of these, individuals <20 cm were collected only within the estuary during otter trawl (n=21, 3.4–19.5 cm) and gillnet (n=1, 16.4 cm) sampling. Alternatively, large numbers of small individuals <20 cm have been collected from the Delaware River and Hudson River estuaries, both known spawning areas (Fig. 2, G and H). Larger juveniles (21–46 cm, presumed age 2–5 years) were better represented in surveys in most locations including the Mullica River–Great Bay estuary (n=55; Fig. 2).

The seasonal patterns of distribution were similar regardless of the spatial scale examined. Individuals 20 to 46 cm, according to the NMFS surveys on the continental shelf, were seldom collected in the fall and winter (a period of restricted sampling in shallow waters) surveys. During the spring (February–March) they were more abundant and largely restricted to the inner portion of the shelf according to composite collections during 1982–2003 (Fig. 3). Most were restricted to an area from north of the Chesapeake Bay mouth to Long Island including the coast of New Jersey.

A similar shallow-water distribution, in space and time, of individuals <46 cm is evident from depth stratified sampling off the coast of New Jersey during all seasons from 1988 through 2003 (Figs. 4 and 5). Both smaller (<20 cm), although less common, and larger (21–46 cm) individuals were most abundant in the spring but also occurred during the winter months and were either rare or absent in the summer and relatively rare during the fall. Over all these seasons, both of these size groups were most abundant in the nearshore depth strata (5.5–9.1 m) with a trend to decreasing abundance with depth with the least number of collections in the offshore strata (18.3–27.4 m). During the winter and spring the larger individuals (21–46 cm) were found all along the coast from the mouth of Delaware Bay to the tip of Sandy Hook (Fig. 5).

Sampling events or tows (n)	Water depths sampled (m)	No. of individuals (<46 cm)	Data source
>16,000	5–481	438	National Marine Fisheries Service; Grosslein and Azarovitz (1982); Able and Brown (2005)
>300,000 (captures); >19,000 (recaptures)	No data	1529 (recaptures)	American Littoral Society; current study
2872	3–80	2930	New Jersey Department of Environmental Protection; Byrne (1989); current study
526	<2	9	Able et al. (2003); current study
2328	0.35–26.0	27	Able and Fahay (2010)
599	0–8	28	Able and Fahay (2010)
243	<2	9	Able et al. (2003); current study
Mobile (80) Passive (>50,000)	1–25	14	Current study
>15,000	1–24	5343	Nemerson and Able (2003); Able et al. (2007)
—	<2	108,445 (1–39 cm)	New York Department of Environmental Conservation

Movements determined with tag-recapture methods

Tagged and recaptured individuals revealed that they could move from natal estuaries to the vicinity of non-natal sources along the New Jersey coast and that those individuals that were found along the New Jersey coast could move to other areas. Few individuals tagged in the nearest natal estuaries (Hudson River and vicinity, n=25, and Delaware River, n=1) were recaptured along the New Jersey coast (n=26 total, Fig. 6A). Small striped bass captured in neighboring natal estuaries ranged in size from 30–46 cm before being recaptured in New Jersey (33–46 cm). Days at liberty for fish captured in nearby natal estuaries ranged from 13–892 (mean 276 days). Individuals tagged in or along the New Jersey coast (n=152 total) were recaptured throughout the northeastern United States from northern Chesapeake Bay (n=4; 3%), Delaware Bay (n=19; 13%), and Long Island and Connecticut (n=27; 18%), with some found as far north as Cape Cod and Maine (n=21; 14%). The majority of recaptures, however, occurred along the New Jersey coast (n=81; 53%; Fig. 6B). The time between capture and recapture was similar for this subset of fish (1–868 days; mean 244 days). For those fish originally captured in New Jersey and recaptured elsewhere along the coast, sizes were generally smaller than in the other subset of fish analyzed and lengths ranged from 25 to 46 cm during capture and from 28 to 46 cm during recapture. A relatively small number of fish were recaptured at sizes less than 40 cm TL (n=18; 11.8%), with all but one of these individuals recaptured less than 100 km from their original release location in New Jersey waters (Fig. 6B).

Estuarine habitat use determined with acoustic telemetry

From 2006 through 2008, 14 small striped bass (32.4–42.5 cm FL) were tagged with acoustic transmitters within the Mullica River–Great Bay estuary in southern New Jersey (Tables 1 and 2, Fig. 7). Most were consistently detected (11 of 14 individuals, n=114 detections) based on mobile telemetry. An examination of the seasonal distribution revealed consistent use of the mesohaline portions of the river all the way up to, and occasionally above, the freshwater-saltwater interface, whereas fewer were found in polyhaline waters near Little Egg Inlet (see Fig. 1). In the summer, fall, and spring some individuals were detected downstream near Little Egg Inlet, or in Great Bay, but during the winter all juveniles were detected upstream in the river (Fig. 7). During December 2006, four fish (42–48 cm FL) were tagged in the ocean off Long Beach Island (Fig. 7C). Of these, one (code 104) moved into the estuary by way of Main Marsh Thorofare (see Fig. 1) on December 24 and remained there for approximately 125 days.

The use of upriver habitats (such as Lower Bank) was evident by the temperature (Fig. 8A) and salinities (Fig. 8B) at which tagged juvenile striped bass were frequently detected. Juveniles inhabited the warmer water temperatures found upstream in the summer

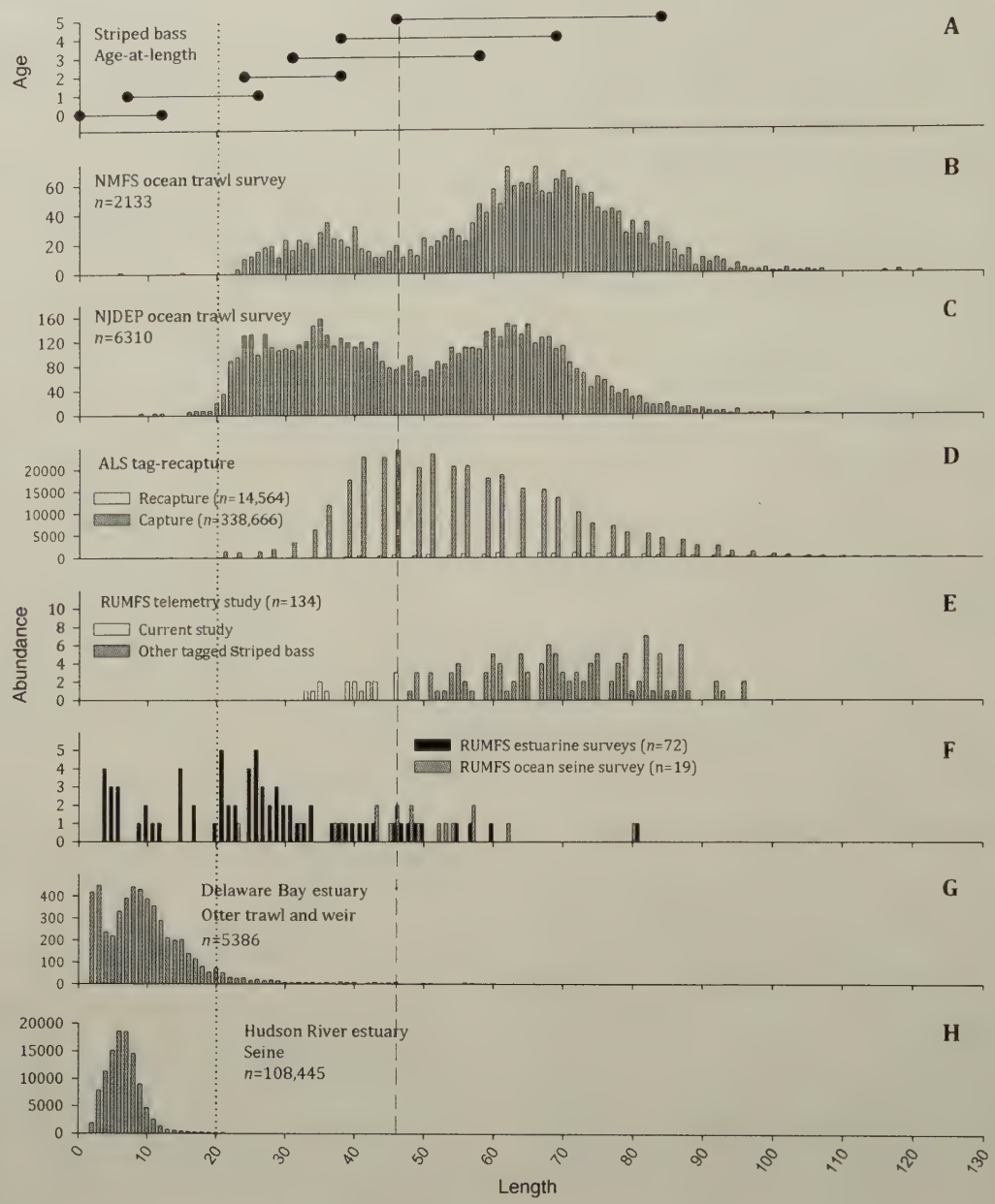

Figure 2

Age (**A**) and length frequency for several continental shelf (**B, C**), estuarine (**E, G, H**), or both (**D, F**) sampling programs. Samples (*n*) reflects total number of striped bass (*Morone saxatilis*) caught. Juvenile striped bass captured during Rutgers University Marine Field Station estuarine surveys shown in (F) include otter trawl (n=28), gillnet (n=31), and seine (n=13) collections. All lengths are expressed as total length (TL), except for (E) which uses fork length (FL). NMFS=National Marine Fisheries Service, NJDEP=New Jersey Department of Environmental Protection, ALS=American Littoral Society, RUMFS=Rutgers University Marine Field Station. See Table 1 for further sampling details.

when the largest temperature gradient occurred relative to downstream areas. In contrast, winter water temperatures were similar at both the inlet and upriver, although fish were detected only upriver. Fish were detected within a wide range of salinities throughout the year. However, most fish were detected within intermediate salinities between the two salinity extremes of the upriver and inlet habitats. The upriver wintertime distribution of tagged individuals revealed a consistent use of lower salinity habitats. These same individuals

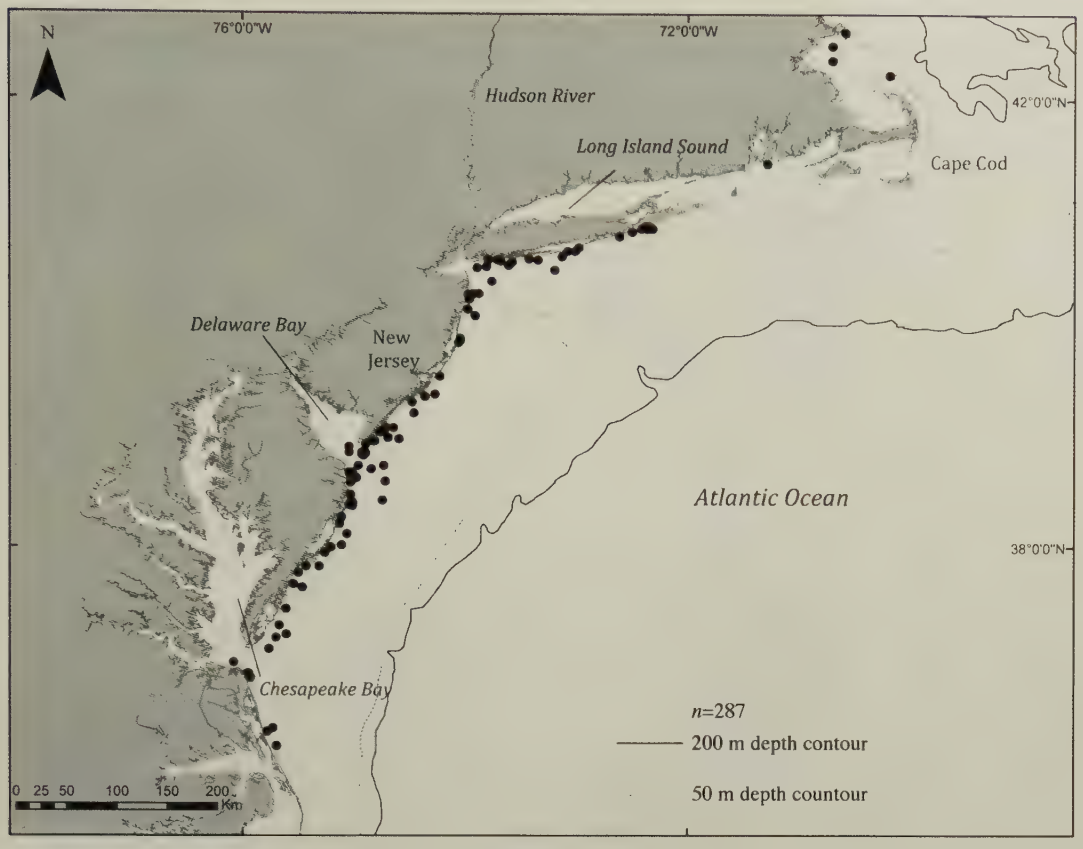

Figure 3

Composite springtime distribution (1982–2003) of small (21–46 cm total length) striped bass (*Morone saxatilis*) north of Cape Hatteras based on National Marine Fisheries Service trawl surveys.

Table 2

Characteristics and detection history of individual acoustically tagged striped bass (*Morone saxatilis*) (<46 cm total length [TL]), in the Mullica River–Great Bay estuary, 2006–08. See Figure 7 for tagging locations: BB=Rutgers University Marine Field Station Boat Basin; LBI=Long Beach Island (Atlantic Ocean); DpPt=Deep Point (Mullica River); DrPt=Doctor's Point (Mullica River); Pkwy=Garden State Parkway Bridge (Mullica River). Seasonal detections are indicated by F=Fall (September–November), W=Winter (December–February), Sp=Spring (March–May), Su=Summer (June–August).

Tag code	Size (cm TL)	Battery life (d)	Tagging location	Tagging date	Mobile tracking detections (*n*)	Passive array detections (*n*)	Seasons detected (mobile tracking)
15	39.4	229	BB	11/12/2007	3	1158	Su
104	41.9	139	LBI	12/11/2006	2	12,926	W Sp
107	41.9	139	LBI	12/11/2006	0	0	—
111	42.5	139	BB	11/16/2006	1	170	Su
113	42.5	139	LBI	12/11/2006	0	0	—
128	34.3	139	DpPt	6/13/2006	0	0	—
132	33.7	139	DpPt	6/13/2006	11	6181	Su
134	35.6	139	DpPt	6/13/2006	6	26,545	F Su
135	40.6	229	DrPt	10/15/2007	15	31,320	F W Sp Su
141	34.3	139	DpPt	6/13/2006	14	344,662	F Su
143	32.4	139	DpPt	6/13/2006	7	95,394	F Su
201	38.7	229	Pkwy	11/14/2007	20	72,096	F W Sp Su
202	38.1	229	Pkwy	11/14/2007	18	24,921	F W Sp Su
209	39.4	229	DrPt	10/15/2007	18	98,040	F W Sp Su

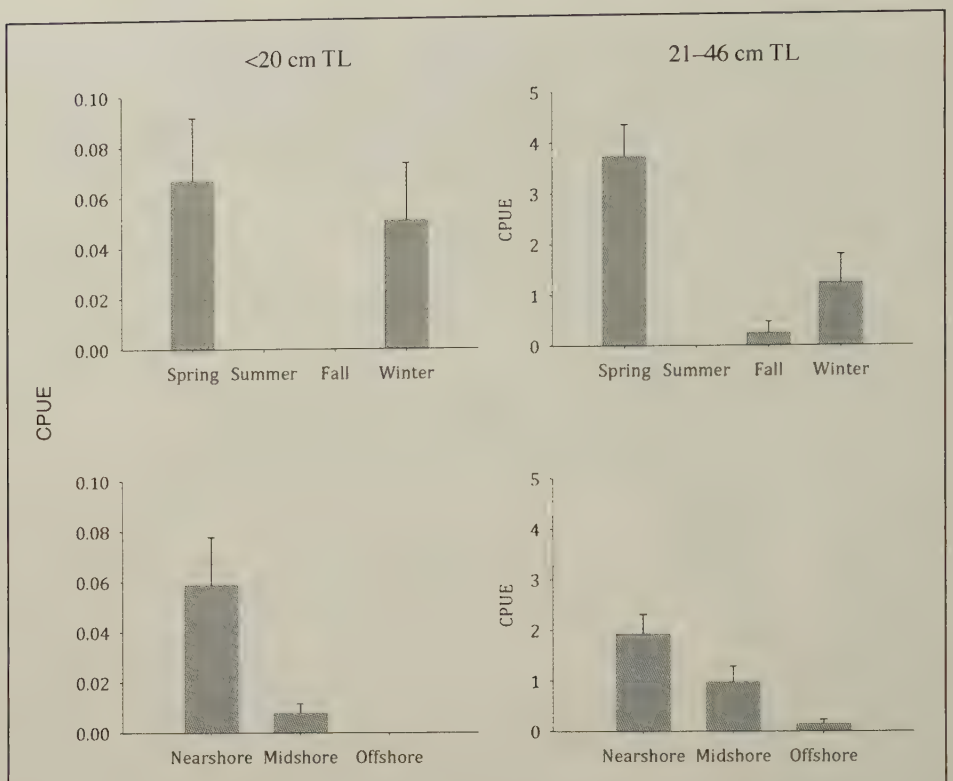

Figure 4

Catch per unit of effort (CPUE) of smaller (<20 cm total length [TL]) and larger (21–46 cm TL) striped bass (*Morone saxatilis*) by season and depth strata (inshore [5.5–9.1 m] mid-shore [9.1–18.3 m], and offshore [18.3–27.4 m]) on the inner continental shelf based on New Jersey Department of Environmental Protection trawl surveys. Error bars represent standard error of the mean. See Figure 5 for description and location of depth strata.

were detected at depths of 0.9–8.3 m (mean 3.6 m). They also showed a differential use of emergent (marsh bank) and submerged (channel edge) embankments across the seasons. Fish were found relatively close to emergent marsh banks across all seasons but were most consistently found there in the spring and fall (85 and 87 m average distances, respectively) and farther away in the summer and winter (190 and 151 m average distances, respectively). Association with channel edges was greatest in the summer (average distance 414 m), and greater average distances were observed during the remaining seasons (1170–1831 m).

Additional tracking based on the passive listening array in this system also detected most (11 of 14, n=713,413 detections) tagged individuals across several seasons (Tables 1 and 2). These were most consistently detected in the Mullica River portion of the estuary (hydrophone nos. 7, 9, 10) but they made movements into the bay (hydrophone nos. 4, 5) as well (see Fig. 1 for locations). One individual (code 141) was resident near hydrophone no. 7 from early summer through fall. Another (code 134) was resident in the bay near hydrophone no. 5 over a similar time period but made occasional movements up to the vicinity of hydrophone 7 in the river. Two other individuals (codes 135 and 201) were resident at hydrophone no. 7 from fall through the following summer but made an initial excursion down into the bay (hydrophone no. 5) and more frequent movements up to the freshwater-saltwater interface near hydrophone no. 10 during the winter. Another individual (code 202) was less frequently detected as it moved from the tagging location in the lower river (hydrophone no. 7) up into the upper river at the freshwater-saltwater interface (hydrophone no. 10) on five occasions during the winter and then back down to the lower river (hydrophone no. 7) later in the spring.

The physical habitat surrounding these extensively used habitats at hydrophones 7 (Chestnut Neck; Fig. 1) and 10 (Lower Bank; Fig. 1) can be similarly characterized by their location within the main stem of the Mullica River (i.e., approximately 250 and 200 m wide, respectively, and adjacency to a channel approximately 4 and 9 m deep, respectively), but these locations vary in aspects of their water quality. Lower Bank is located at the freshwater-saltwater interface of the Mullica River–Great Bay estuary (daily average 3.3 ppt, range: 0.0–17.7 during 2006–08) and Chest-

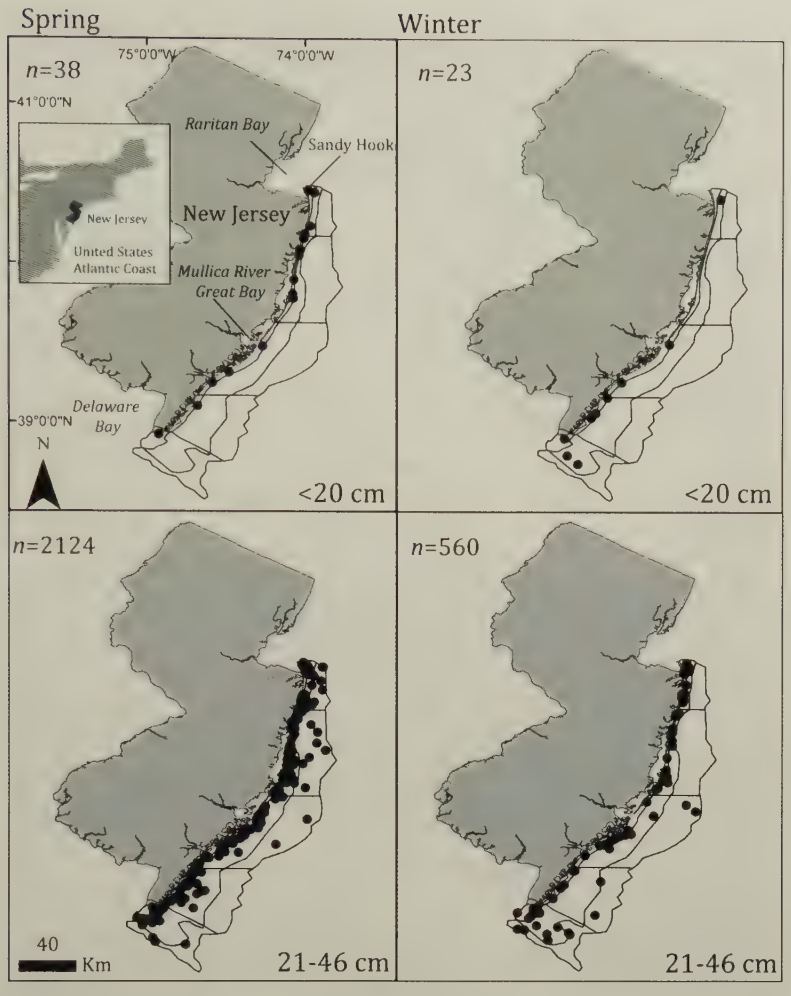

Figure 5

Composite spring and winter distributions for two size classes of small striped bass (*Morone saxatilis*) (<20 cm total length [TL] and 21–46 cm TL) at multiple depth strata (inshore [5.5–9.1 m], midshore [9.1–18.3 m] and offshore [18.3–27.4 m]) on the New Jersey inner continental shelf based on New Jersey Department of Environmental Protection trawl surveys.

nut Neck is characterized by intermediate salinities (daily average 15.2 ppt, range: 0.2–29.7 during 2006–08). Lower pH values (daily average: 6.1, range: 3.4–8.5 during 2006–08) are also present at Lower Bank due to the natural influx of tannins from the surrounding watershed, whereas Chestnut Neck experiences more neutral pH levels (daily average: 7.4, range: 5.2– 8.5 during 2006–08) moderated by the effect of incoming ocean and bay waters. Dissolved oxygen (DO) levels never reached anoxia during the study period at either hydrophone site. However, in the summer of 2006, DO dropped to hypoxic levels during short periods of the day at hydrophone nos. 7 and 10 (0.2 and 0.8 mg/L, respectively). Otherwise, daily mean DO levels remained relatively high and were similar throughout the study period at both sites (Lower Bank daily average: 9.0 mg/L; Chestnut Neck daily average: 8.8 mg/L).

Discussion

Sources of striped bass for non-natal estuaries

The assumption has long been that the sources of small striped bass that occur along the New Jersey coast and in non-natal estuaries have been major river estuaries to the north (Hudson River: Dovel, 1992; Secor and Piccoli, 1996; Dunning et al., 2009) and south (Chesapeake Bay: Mansueti, 1961; Kohlenstein, 1981; Dorazio et al., 1994) including the Delaware River (Waldman and Wirgin, 1994; Weisberg et al., 1996). This interpretation has become accepted because there are no accounts of reproduction in other systems between Cape Cod and Cape Hatteras (Collette and Klein-MacPhee, 2002; but see Little, 1995). This interpretation is further supported by the large number of small juveniles (<20 cm) encountered in Delaware Bay in the last decade (Able et

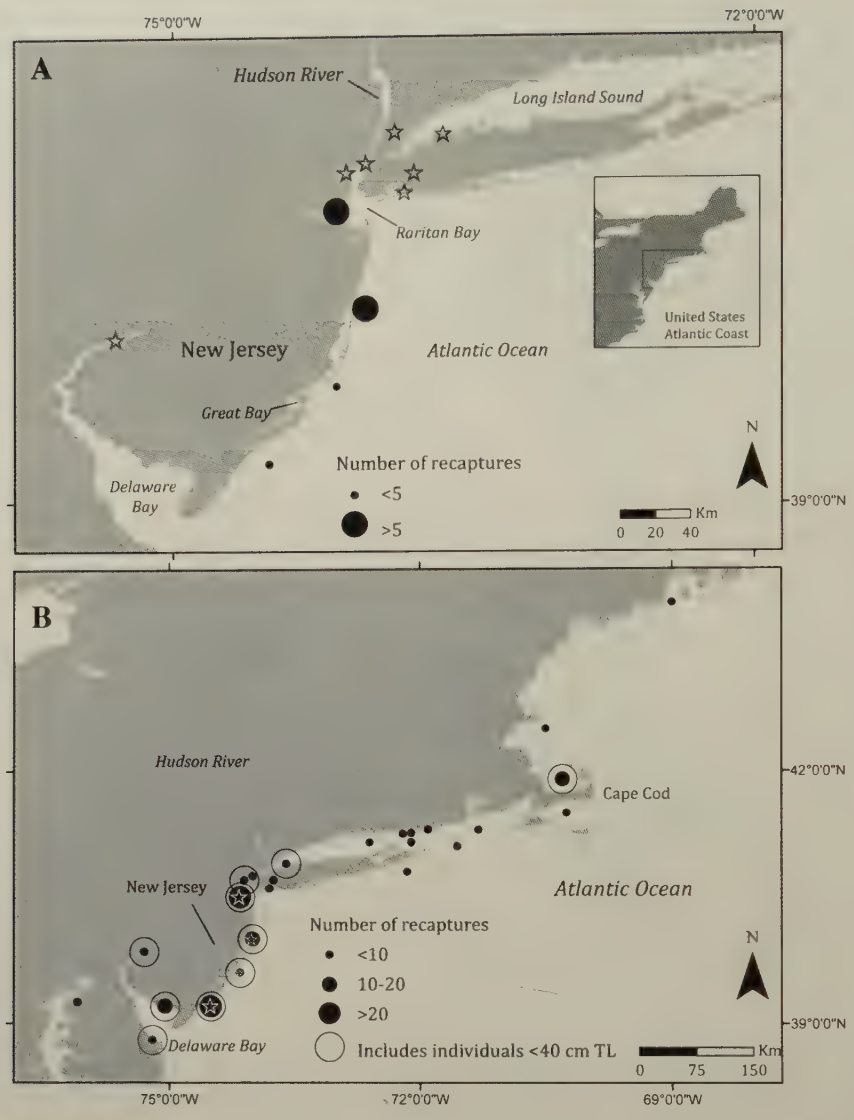

Figure 6

Spatial distribution and abundance of recaptures of small (<46 cm total length [TL]) striped bass (*Morone saxatilis*) tagged during the American Littoral Society tagging program (**A**) near potential source (natal) populations in the Hudson River estuary (including New York Harbor, Jamaica Bay, and western Long Island Sound) and the Delaware Bay and recaptured along the ocean coast of New Jersey, and (B) near potential non-natal sources along the ocean coast of New Jersey and recaptured along the Atlantic coastline. Circled recaptures shown in (**B**) represent fish recaptured at less than 40 cm TL.

al., 2007), as well as by data (Fig. 2) and many studies in the Hudson River (Hurst and Conover, 1998; Hurst et al., 2000; Dunning et al., 2009; Fig. 2) and Chesapeake Bay (Mansueti, 1961). Further, the tag-recapture data for small striped bass reported along the coast of New Jersey support the interpretation of movement from the Hudson River and Delaware Bay. Although there are movements of some ultrasonically tagged adults up to the freshwater-saltwater interface, as if for spawning, in the Mullica River–Great Bay estuary (Able and Grothues, 2007; Grothues et al. 2009), very few small individuals less than 20 cm (n=27) have been collected there despite intensive sampling over two decades (Table 1).

It is difficult to evaluate whether the sources of small striped bass have changed since the recovery in the 1980s (Wooley et al., 1990; Richards and Rago, 1999). Clearly the major estuaries that support natal populations appear to be the same, i.e., Chesapeake Bay and its tributaries and the Hudson River. It is

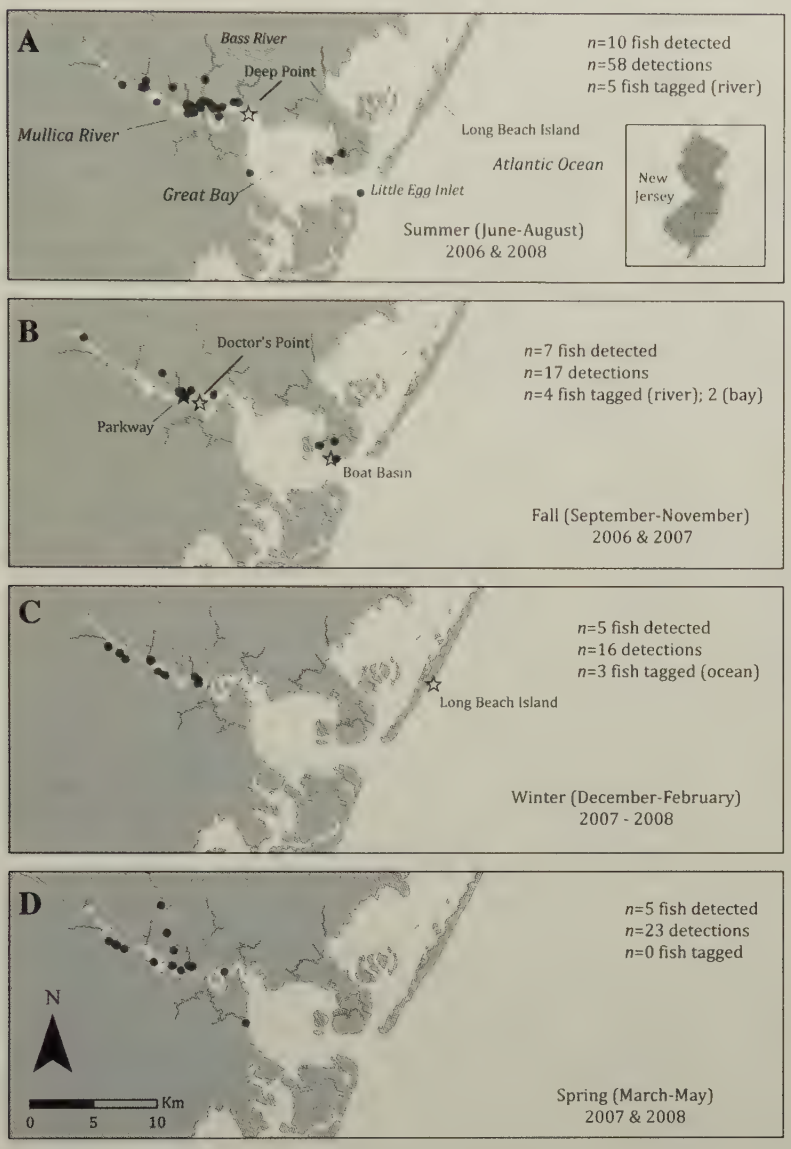

Figure 7

Seasonal tagging locations and distributions of ultrasonically tagged small (<46 cm total length) striped bass (*Morone saxatilis*) in the Mullica River-Great Bay estuary based on mobile telemetry during the (**A**) summer, (**B**) fall, (**C**) winter, and (**D**) spring. See Figure 1 for locations mentioned in the text.

also clear that the Delaware River population is distinct (Waldman and Wirgin, 1994) and has recovered (Weisberg et al., 1996) on the basis of the large number of juveniles in the system (Nemerson and Able, 2003; Able et al., 2007). Also, movement of juveniles from the coast of New Jersey determined with the ALS tag-recapture data, is consistent with earlier patterns (Boreman and Lewis, 1987) in that most recaptures are found to the northeast of the New Jersey tagging sites.

A second assumption has been that young-of-the-year and small juveniles remain in the natal estuary for several years until they begin moving into the ocean and making coastal migrations (Merriman, 1941; Zlokovitz et al., 2003). However, in the Hudson River, movement out of the estuary by postyolksac larvae (Dunning et al., 2009) and age 0, 1, and 2 juveniles (McKown[5]; Dovel, 1992) could account for the occurrence of small striped bass in non-natal estuaries. This dispersal of small juveniles (<20 cm) is not detected in NMFS surveys (n=2), despite the intensive sampling

[5] McKown, K. A. 1991. An investigation of the movements and growth of the 1989 Hudson River year class. *In* A study of the striped bass in the marine district of New York, 2010, p. 5. NY State. Dep. Environ. Conserv., Albany, NY.

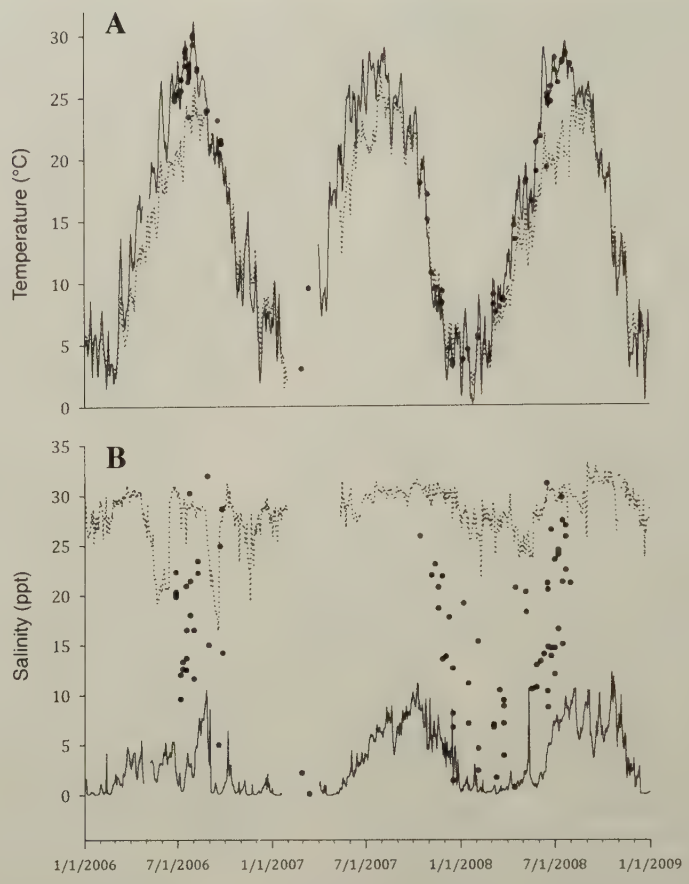

Figure 8

Daily mean (**A**) temperature (°C) and (**B**) salinity (ppt) profiles from the Mullica River–Great Bay as collected by the Jacques Cousteau National Estuarine Research Reserve System-Wide Monitoring Program's Buoy 126 near Little Egg Inlet (dashed line) and Lower Bank (dark continuous line) water quality data loggers from 2006 through 2008 (see Fig. 1 for locations). Filled black circles represent the temperature and salinity values at locations where ultrasonically tagged small (32.4–42.5 cm total length) striped bass (*Morone saxatilis*) were detected during mobile telemetry tracking efforts during the same time period.

(Table 1), in part, because these small individuals remain in shallow coastal waters where they are not available to these surveys (Figs. 2 and 3). However, a few of this size have been detected along the shallowest depth strata along the coast of New Jersey in NJDEP otter trawl and RUMFS ocean beach surveys (Figs. 2, 4, and 5). At these sizes they can be detected in the winter and spring as they move out of the estuaries. Further support for these movements occurs in the tag-recapture observations of small striped bass that are captured in potential natal estuaries and disperse to other areas along the New Jersey coast (Fig. 6). Thus, dispersal of young-of-the-year and other small juveniles from natal estuaries such as the Hudson River estuary, Delaware Bay, and even the Chesapeake Bay (possibly through the C and D Canal; Fig. 1) could account for the smaller individuals (<20 cm) that occur in the non-natal Mullica River–Great Bay estuary (Fig. 2) because of the absence of successful spawning there (Able and Grothues, 2007; Grothues et al., 2009).

The motivation for leaving the natal estuary and the primary nursery, regardless of whether they are partial migrants or entrained (Secor and Kerr, 2009), has been attributed to age (Kohlenstein, 1981), exploration due to density dependence (Secor and Kerr, 2009), and sex specific variation (i.e., females tend to leave and males tend to stay) (Kohlenstein, 1981). What is not clear is what motivates small striped bass to enter and become resident in non-natal estuaries, although optimal re-

sources (e.g., food, benign environmental conditions) are likely causes (e.g., Mather et al., 2009). Further, the long duration of their stay in a non-natal estuary enhances the possibility of learning behavior at a young age that may lead to contingent formation (Secor, 1999).

Distribution and habitat use in a non-natal estuary

Once small striped bass dispersed into the estuary at Mullica River–Great Bay, regardless of the source of these individuals, a large proportion of them took up residence there for months. Their residency is evident by their presence in the system during all seasons (Table 2, Fig. 7). During this time they were most frequently observed in the Mullica River but less frequently in Great Bay. This is a very different pattern from that of the larger juveniles and adults who are typically present only seasonally in this estuary, particularly during the spring and fall (Able and Grothues, 2007; Grothues et al., 2009). It is consistent with the interpretations of coastal migrations by the larger and older individuals through non-natal estuaries, as also occurs in Massachusetts (Mather et al., 2009; Pautzke et al., 2010).

As a result of our analysis, based on multiple spatial scales and multiple techniques, it seems clear that the Mullica River–Great Bay estuary, and probably other non-natal estuaries in the Middle Atlantic Bight, are commonly used by small striped bass that disperse from natal estuaries and take up residence in this and other non-natal estuaries (Able and Fahay, 2010). Thus, should these non-natal estuaries be considered nurseries? A reevaluation of the nursery concept (Beck et al., 2001) and subsequent dialogue (Dahlgren et al., 2006; Sheaves et al., 2006; Fodrie et al., 2009) clarify several points regarding this question. First, we do not know whether the pattern of dispersal to and colonization of the non-natal Mullica River–Great Bay estuary is common to other non-natal estuaries and whether this colonization is accomplished by immature or maturing individuals. Second, if colonization does occur commonly, we do not know the degree of the contribution of these individuals to adult reproduction or population growth, in part, because there are so few studies of the dispersal of young striped bass (<20 cm), or any species, out of estuaries (Deegan, 1993; Beck et al., 2001; Gillanders et al., 2003). Third, it should not be surprising that a mosaic of habitats (e.g., Sheaves, 2005; Sheaves et al., 2006), including non-natal estuaries, is used by striped bass, and other species (Gillanders et al., 2003; Dahlgren et al., 2006) and the complexity of the mosaic may influence population growth (e.g., Fodrie et al., 2009) and add to a population's buffering capacity against unfavorable habitat dynamics (e.g., Secor, 2007). One possible solution is to consider natal estuaries, and their subsequent use by young-of-the-year and small juveniles, as primary nurseries and non-natal estuaries as secondary nurseries for slightly older individuals. This approach has been useful in identifying shark nurseries (Bass, 1978; Merson and Pratt, 2007).

Egress from a non-natal estuary

It appears that small striped bass leave non-natal estuaries, such as the Mullica River–Great Bay system, to begin coastal migrations at the same sizes as those in natal estuaries. This departure of juveniles to become coastal migrants may vary after months, to perhaps years, of residency. Others have suggested that movement from natal estuaries to join the coastal migration may be size or age related such that juveniles may begin to leave estuaries after two years (Merriman, 1941; Kohlenstein, 1981; Setzler-Hamilton and Hall, 1991; Secor and Piccoli, 1996; Zlokovitz et al., 2003). It is known that egress from Chesapeake Bay by immature females occurs in early spring at age 2 and 3 (Merriman, 1941). These patterns are consistent with the occurrence of striped bass of similar sizes along the coast determined by tag-recapture of striped bass in the ALS tagging program. For instance, a majority of fish recaptured along the coast of New Jersey after release in natal estuaries were larger individuals (>40 cm TL) that may be joining the annual coastal migration. These larger individuals were also frequently recaptured in presumably non-natal habitats in the Gulf of Maine and along the coasts of Connecticut and Rhode Island after initial release in New Jersey waters. This same pattern has been reported for age 2 and 3 fish moving into non-natal estuaries, such as the Connecticut River (Kynard and Warner, 1987) and in Massachusetts where 40–50 cm TL individuals (most age 2–5) apparently feed during the summer, make coastal migrations during the fall through spring, but return in subsequent years (Mather et al., 2009, 2010; Pautzke et al., 2010). Certainly, other estuarine-dependent fish species leave estuaries when they reach a size threshold (Rountree and Able, 1992; Potter et al., 1997). This pattern for striped bass may vary with sex, i.e., females are likely to leave at earlier ages or smaller sizes, whereas males tend to remain, at least in natal estuaries, for longer periods of time (Secor and Piccoli, 1996).

In general, overall patterns of use of a non-natal estuary and scheduling of departure appear similar between natal and non-natal estuaries and we also suspect that there are no major changes in these patterns before and after the recovery of the striped bass population in recent years (Boreman and Lewis, 1987). However, we hasten to point out that there was little emphasis on non-natal estuaries as secondary nursery habitat before the recovery.

Conclusion

As we have demonstrated, non-natal estuaries are potentially important habitat for small (20–46 cm) striped bass. This finding may further complicate our understanding of life cycle diversity (see Secor and Kerr, 2009) for this species because the prior focus has been on natal estuaries. Further, as these individuals from non-natal estuaries join the annual coastal

migration, grow, and mature, one wonders where they are likely to spawn. One possibility is that they will attempt to spawn in the non-natal estuaries where they have previously spent several months to years. This could account for the seeming unsuccessful attempts in the Mullica River–Great Bay estuary (Able and Grothues, 2007; Grothues et al., 2009). One could also argue that these individuals may be responsible for colonizing new spawning sites, as has previously been suggested (Grothues et al., 2009). Alternatively, they may join other maturing individuals as they migrate back to their natal rivers and streams that provided primary nurseries. Otolith microchemistry might be the appropriate means to distinguish the ultimate source of individuals that use non-natal estuaries and the site of their subsequent spawning.

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Prey preference of lingcod (*Ophiodon elongatus*), a top marine predator: implications for ecosystem-based fisheries management

Craig A. Tinus

Email address for contact author: craig.tinus@oregonstate.edu

Oregon State University
Department of Fisheries and Wildlife
104 Nash Hall
Corvallis, Oregon 97331-3803

Present address: Oregon Department of Fish and Wildlife
Corvallis Research Lab
28655 Hwy 34
Corvallis, Oregon 97330

Abstract—Many highly exploited ecosystems are managed on the basis of single-species demographic information. This management approach can exacerbate tensions among stakeholders with competing interests who in turn rely on data with notoriously high variance. In this case study, an application of diet and dive survey data was used to describe the prey preference of lingcod (*Ophiodon elongatus*) in a predictive framework on nearshore reefs off Oregon. The lingcod is a large, fast-growing generalist predator of invertebrates and fishes. In response to concerns that lingcod may significantly reduce diminished populations of rockfishes (*Sebastes* spp.), the diets of 375 lingcod on nearshore reefs along the Oregon Coast were compared with estimates of relative prey availability from dive surveys. In contrast to the transient pelagic fishes that comprised 46% of lingcod diet by number, rockfishes comprised at most 4.7% of prey items. Rockfishes were the most abundant potential prey observed in dive surveys, yet they were the least preferred. Ecosystem-based fisheries management (EBFM) requires information about primary trophic relationships, as well as relative abundance and distribution data for multiple species. This study shows that, at a minimum, predation relative to prey availability must be considered before predator effects can be understood in a management context.

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Ecosystem-based fisheries management (EBFM) has generated considerable interest over the last decade as a way of better managing depressed fisheries stocks (Pikitch et al., 2004; Gaichas et al., 2010). This interest has been in large part a reaction to the perceived failure of traditional single-species fisheries management to prevent the collapse of exploited and ancillary populations in many systems worldwide (Dulvy et al., 2003; Hutchings and Baum, 2005; Myers and Worm, 2005). One implication of EBFM is the capacity to forecast changes in managed populations in reaction to fluctuations in linked predator and prey populations. This requires understanding what species of interest consume in a given temporal and spatial context. An additional consideration is that many exploited fishes are generalist consumers and shifts in densities and distributions may produce complex top-down effects (Bruno and O'Connor, 2005). These are among numerous challenges in gathering the information required to describe even a subset of primary trophic relationships in a dynamic system.

Prey preference is the differential consumption of some prey types over others given equal availability. It is considered a fixed behavioral characteristic and, as a way of forecasting predation intensity on managed stocks, has received little attention. However, preference models may be both useful and efficient as an extension of food web models to aid management of exploited stocks (Gaichas et al., 2010). In this study I used an analysis of dive survey data with consumption data in a prey preference model to better understand the likely effects of a rapidly increasing predator population on managed prey. Consumption rates for generalist consumers like lingcod (*Ophiodon elongatus* Girard) may be either positively or negatively correlated among different prey types, or they may be uncorrelated, and these effects can be important in actively managed systems (Dill et al., 2003). If spatially and temporally transient prey species predominate in the diet of a resident predator, they may constitute subsidies to the local predator population (Anderson and Polis, 1998). When subsidies occur there may be a concomitant suppression of local prey species through apparent competition among prey types with a common predator (Holt, 1977; Chaneton and Bonsall, 2000). Especially in marine systems where trophic webs may be poorly defined (Thompson et al., 2007), initial consideration of predator-prey relationships requires dietary analysis (Heithaus et al., 2008). Diets of targeted fishery species provide necessary information for understanding food web structure, which is an important requirement for ecosystem-based fisheries science

and management (Francis et al., 2007). However, in addition to these basic trophic relationships, it is necessary to understand the context in which prey are being selected. The effects of predation on both predator and prey populations change as prey densities vary.

Although EBFM requires even more information than traditional single-species management approaches, managers, scientists, and stakeholders make use of less certain information both in less accessible systems and in those that are accessible but where temporal and spatial scales far exceed the capacity to collect local demographic data. For these reasons identifying specific management triggers based on comprehensive and collectable information has been proposed (Samhouri et al., 2010) and the case made that uncertain data and imperfect advice must be embraced, as long as they are appropriate data (Ludwig et al., 1993; Johannes, 1998; Frid et al., 2008). Challenges to the use of EBFM include "species conflicts," where management and stakeholder interest in one target species may interfere with other species and often involve the assumed effects of large generalist predator(s) on recovering high value prey species, sometimes in and out of marine protected areas. Examples of generalist predators involved in management conflicts are groupers (*Epinephelus* spp. [Ault et al., 2006; Coleman and Koenig, 2010]), red snapper (*Lutjanus campechanus* [Wells et al., 2008; Cowan et al., 2010]), cod (*Gadus morhua* [Link and Garrison, 2002]), and striped bass (*Morone saxatilis* [Paolisso, 2002; Walter et al., 2003]).

Marine reserves are becoming more widely considered as a management tool for protecting a portion of breeding populations as interest in EBFM increases. However, in addition to providing a refuge from fishing mortality, marine reserves can enhance local populations of large, resident, top-level predators (Martell et al., 2000; McClanahan and Arthur, 2001). Among possible effects of a local increase in predator biomass is a decrease in a particular prey type (Graham et al., 2003). For example, this kind of interaction has been proposed for lingcod predation on rockfishes (*Sebastes* spp.) within marine reserves (Beaudreau and Essington, 2007; 2009) and both are major targets of commercial fisheries.

The following case study exemplifies necessary considerations for EBFM. Lingcod are targeted by both recreational and commercial fishermen along the west coast of North America. The 2000 stock assessment of lingcod from British Columbia to northern California estimated biomass at 11% of precommercial exploitation levels (Jagielo, et al.[1]) and management substantially reduced fishing mortality to allow recovery of this stock. By 2006, lingcod stocks were declared fully recovered by the Pacific Fisheries Management Council. Lingcod are large (up to 152 cm total length [TL] and 59 kg) and fast growing. They are relatively site-attached, demersal, generalist predators, found on shallow northeastern Pacific rocky reefs. They roam across both rocky habitat and soft-bottom over distances of at least hundreds of meters, yet they demonstrate a high degree of site fidelity for time scales of at least weeks to months (Jagielo, 1990; Smith et al., 1990; Mathews, 1992; Yamanaka and Richards, 1993; Jagielo, 1999; Starr et al., 2004).

Although lingcod population dynamics have been studied from a fisheries perspective, very little is understood about how this predator affects the structure of fish populations and assemblages on rocky reefs. A previous study of diet and habitat associations of demersal fishes on nearshore reefs along the Oregon Coast revealed that 282 adult lingcod had consumed 27 identifiable species of fish and invertebrates. Of those 134 prey items, no adult rockfishes were found and the contribution to total biomass by all rockfish prey was less than one percent (Steiner, 1979). However, no prior lingcod studies have described diet in relation to prey abundance. In order to assess differential selection, and thus characterize which prey types will most likely be selected, there must be an estimate of prey availability relative to consumption (Manley et al., 2002). The goal of this study was to describe the diet of adult lingcod off the coast of Oregon, to characterize relative patterns of consumption of transient and resident prey species by lingcod, and describe whether or not preference, defined as the differential consumption of one prey type over others in relation to availability, was evident. Specifically, by using lingcod diet and prey abundance estimates off the coast of Oregon, I addressed the following questions: 1) Do lingcod prefer particular prey species, and 2) do lingcod preferentially target rockfishes? The answers to these questions were yes and no, respectively. This information can be used to more effectively manage a reserve system where both predator and prey populations are the focus of conservation efforts.

Materials and methods

Study area

The nearshore zone off Oregon is generally exposed, has relatively high wave energy, and is influenced by longshore currents. I sampled lingcod from two nearshore subtidal sites along the coast of Oregon: one south of Newport, referred to as site 1 (44°31′N lat.; 124°08′W long.), and another south of Coos Bay, referred to as site 2 (43°16′N; 124°25′W) (Fig. 1). Both sites comprised high relief rocky reef, rocky flats, cobble, and sand at depths of 20 to 50 m. The reefs varied from small pinnacles encompassing <10 m^2 to large boulder fields and bedrock flats that may exceed one km^2 in area. The area of exposed rock changes on temporal scales of months to decades, however, sand transport is greatest during the stormy winter months and relatively stable during the summer (Kulm et al., 1968).

[1] Jagielo, T. H., F. R. Wallace, and Y. W. Cheng. 2003. Assessment of lingcod (*Ophiodon elongatus*). Amendment 16-2: Rebuilding plans for darkblotched rockfish, Pacific ocean perch, canary rockfish, and lingcod. Environmental impact statement and regulatory analysis, 129 p. Pacific Fishery Management Council, Portland, OR.

Prey availability

Prey availability was compared with observed prey consumption to evaluate prey preference. Lingcod are highly generalized visual predators and visual surveys provide an estimate of relative prey density within a visual field. I evaluated prey availability with dive surveys in the areas where lingcod were collected for gut analyses (Starr et al., 2010). Dive surveys were conducted from a relatively small boat equipped with standard electronics. Ocean conditions had to be sufficiently benign for both safe boat handling and diver deployment and recovery. Weather conditions were a limiting factor for dive surveys. In general, combined seas (wave and swell height) of less than two to three meters and wind velocities of less than 20 knots are necessary. Additionally, fog and strong currents at times prohibited safe dive and boat operation near shallow reefs. A single dive survey consisted of a single 100×4 m visual-count transect (Bohnsack, 1996) during daylight between 1000 and 1500 hours. I conducted surveys at site 1 in January and June 2004, and in June 2005 (three surveys total), and at site 2 in January and October 2004, and in June (three surveys) and September 2005 (six surveys total) (Table 1). The exact locations of transects were determined haphazardly from the surface by dropping a weighted line in an area as close as possible to where fishing for lingcod occurred and where depths were sufficiently shallow so that single dive surveys could be completed within one scuba dive (<35 m). Visibility was variable but was always sufficient to identify fish within two meters of the transect line, and fishes and invertebrates were approachable. I surveyed three basic habitat types within each transect: high-relief rocky reef, boulder mixed with cobble, and broken shell mixed with sand. I quantified the relative abundance of potential prey within the foraging range of lingcod, estimating age groups of rockfishes (year 1, 1–2, 3+) from estimated total lengths. During dives I estimated fish lengths by comparing them against objects of similar shape and color of known lengths at various distances. I observed only adult lingcod on rocky reef habitat. Relative prey availability between sites 1 and 2 were compared by one-way analysis of similarity (ANOSIM; Clark, 1993). The ordination, associated tests, and species accumulation curves were produced with PRIMER analytical software (vers. 6.1.6, PRIMER-E Ltd., Plymouth, U.K.[2]) by using an included ANOSIM method (Clark and Gorley, 2006). Additionally, a rank concordance test of prey category abundance was conducted for sites 1 and 2 (Sokal and Rohlf, 1995). For comparisons of two groups, *t*-tests were used unless a Shapiro-Wilk test for normality, equal variance, or both, failed, in which case a Mann-Whitney rank sum test was used. The Michaelis-Menten equation (MME) was used to generate species accumulation curves to evaluate how quickly the number of new species became asymptotic (curve stability) with additional sampling effort (Willott, 2001; Williams et al., 2007). The beta value for the MME represents the number of samples required to detect 50% of the total number of species, or groups.

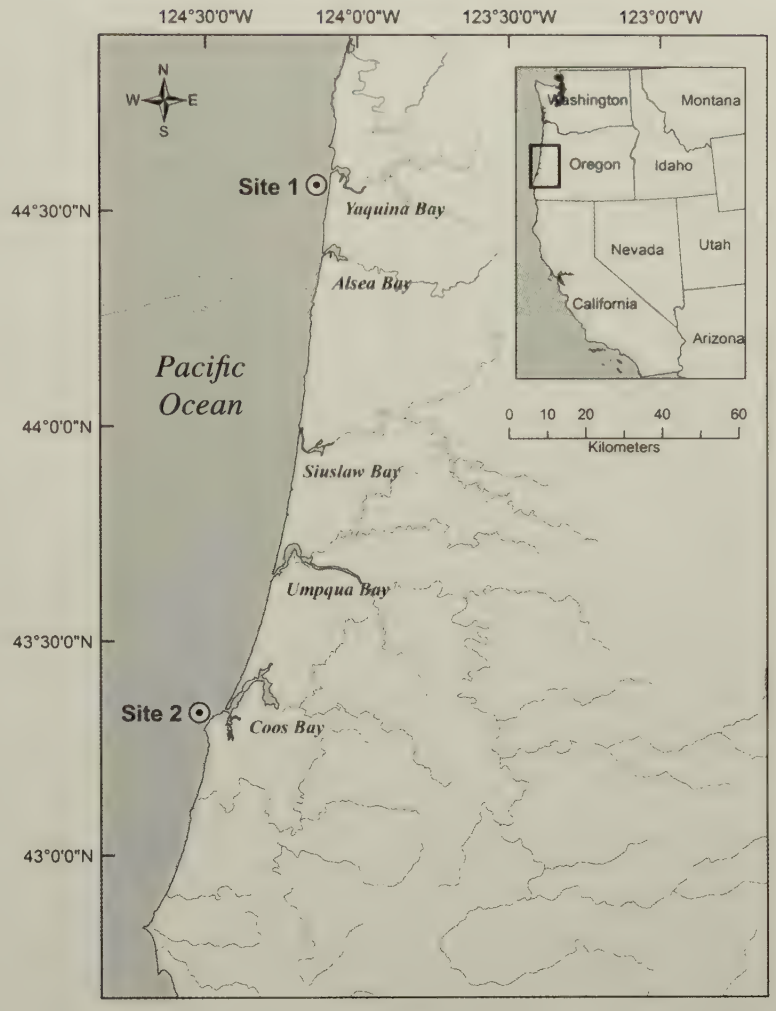

Figure 1

Map of study region (inset) and study sites (1 and 2) within the Oregon nearshore zone where stomach samples of lingcod (*Ophiodon elongatus*) were collected and dive surveys of potential prey were conducted.

Dietary composition

Multiple anglers using lines with a single hook and attractor on a chartered recreational fishing vessel in July (19 and 17 fish in two sampling trips), August (12 fish), and September (12 fish) of 2003 (one trip each) collected a total of 60 lingcod at site 1. The lingcod collected at Site

[2] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

2 were by a commercial fisherman in the months of May (21 fish), June (48 fish), and October (59 fish) of 2004, and May (49 fish), June (45 fish), August (46 fish), and October (40 fish) of 2005 (Table 1). The commercial gear used was a "dingle-bar"—an iron bar trolled just off the seafloor with a set of three rubber jigs with large hooks and an attractor. An additional set of three jigs with hooks was trolled mid-water (about 10–20 m off-bottom). When multiple lingcod hit the jigs, they generally did so simultaneously on both the bottom and mid-water sets.

In the first year, lingcod stomachs were labeled, placed in cloth bags, and preserved in ethanol. In subsequent years, stomachs were labeled, wrapped in cheesecloth, packed in ice, and examined within 24 hours. The number and identity of items in each stomach were identified to the lowest possible taxon. When the identification of a prey fish was not possible from external characteristics, I attempted to identify the prey by otoliths or skeletal elements (or both). A second, blind reading of a subsample of otoliths and skeletal elements was done by a recognized expert who confirmed prior determinations. When possible, beaks were used to estimate size and infer species of octopus by comparison with other samples that were identified to species from external characteristics.

Observed consumption provides a description of a local prey base if sample sizes are large enough to capture the diversity within a population and incorporate representative temporal and spatial scales. Although lingcod are highly generalized, the incidence of new prey types in gut samples was asymptotic with increasing sample size. The MME was used to generate a species-accumulation curve and test for sufficiency of sampling effort. A rank concordance test of prey category abundance was conducted for sites 1 and 2 (Sokal and Rohlf, 1995). For comparisons of two groups, *t*-tests were used unless a Shapiro-Wilk test for normality or equal variance test (or both) failed, in which case a Mann-Whitney rank sum test was used. Additionally, one-way analysis of variance (ANOVA) was used to test for differences among sampling trips for differences in stomach fullness and for differences in consumption of transient and resident prey types.

Stomach content data were analyzed by frequency of occurrence, $\%F_o = (n \cdot 100)/N_s$; and percentage of prey, $\%N = (n'-100)/N_p$; where n=the number of stomachs containing a particular prey type, N_s=the total number of lingcod stomachs examined, n'=the total number of individuals of a particular prey type, and N_p=the total number of prey items (Hyslop, 1980).

Table 1

Dates and locations of dive surveys and stomach collections for diet samples of lingcod (*Ophiodon elongatus*) in the nearshore zone off the Oregon Coast. Site 1 is located south of Newport, OR, and site 2, south of Coos Bay, OR. An X indicates that data were collected. Data used for prey preference analysis are within-season.

Dive survey	Diet samples	Site	Date
	X	1	16/07/03
	X	1	23/07/03
	X	1	25/08/03
	X	1	24/09/03
X		1	09/01/04
X		2	22/01/04
	X	2	24/05/04
X		1	09/06/04
	X	2	24/06/04
	X	2	05/10/04
X		2	22/10/04
	X	2	13/05/05
X		2	03/06/05
	X	2	08/06/05
X		1	22/06/05
X		2	26/06/05
X		2	27/06/05
	X	2	17/08/05
X		2	28/09/05
	X	2	20/10/05

Prey-preference model

A preference model describes the relative selection of resources in relation to the availability of those resources. If a particular prey type is selected more or less frequently than would be predicted by relative availability, that prey type is said to be either preferred or avoided relative to other prey types. The general formulation of the preference model (Johnson, 1980) is as follows. Let r_{ij} be the rank of some measure of consumption of prey component (i) by an individual predator (j) and s_{ij} be the rank of an observed measure of the availability of prey component (i) to individual predator (j). The individual differences in these ranks, $t_{ij} = r_{ij} - s_{ij}$, are then averaged across animals to indicate the relative preference of all prey types across all predators, as given in Equation 1 below. The advantage of this nonparametric approach is that information about prey preference can be gleaned from imperfect field data. The use data and availability data are ranked for each animal and even if a particular prey type is not observed, those data can be used in the analysis. If a known prey type was not observed, the availability of that particular prey type would be considered low by comparison with other prey types in the analysis.

$$\bar{t}_i = \sum_{j=1}^{J} (r_{ij} - s_{ij}) / J. \quad (1)$$

Results

Prey availability

Observed fish abundance was overwhelmingly dominated (over 90%) by demersal rockfishes (*Sebastes* spp.) at both

sites. Aggregations of black rockfish (*S. melanops*) typically exceeded 100 individual adults and were the most common rockfish species. There was no evidence of a group effect between sites 1 and 2 (one-way ANOSIM, global R=–0.115; significance of sample stat.=64.2%). An MME for species accumulation indicated sampling effort was sufficient to achieve a stable asymptotic curve (S_{max}=17.94; β=0.72). In the pooled data, black rockfish were 41.1% of a total of 2640 fish recorded in nine dive surveys. When *Sebastes* species were aggregated into a single prey category (demersal rockfishes) there was no difference in mean abundance between sites (two-sided t-test, P=0.84, df=7) or of lingcod abundance between sites (Mann-Whitney U=26.5, P=1.0). There was a mean of 177.7 (standard error [SE]=14.8) demersal rockfish and 4.3 (SE=0.33) lingcod observed at Site 1 and a mean of 148.8 (SE=37.8) rockfish and 3.8 (SE=0.98) lingcod at site 2. A rank concordance test of prey common to both sites was significant with respect to abundance of potential prey species between sites (Kendall's rank concordance test, P<0.01, n=16, s=1.91). Striped surfperch (*Embiotoca lateralis*) and yellowtail rockfish (*S. flavidus*) were recorded only at site 1, whereas canary rockfish (*S. pinniger*) were observed only at site 2. Besides those species, the sites did not differ with respect to either the presence of potential prey species or relative abundance by genus, with the exception of significantly more sculpins (family Cottidae) at site 1 than site 2 (Mann-Whitney U=18.0, P=0.3). Geographic ranges of all species in this study are known to overlap both sites.

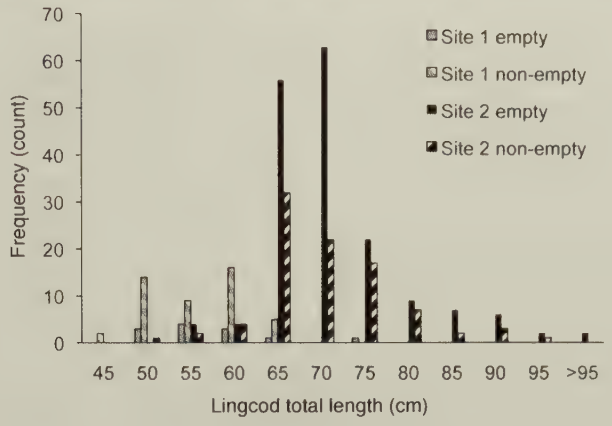

Figure 2

Lingcod (*Ophiodon elongatus*) total length (cm) and frequency of occurrence for empty and nonempty stomachs sampled at sites 1 and 2 off Oregon, 2003–05. Gear types were: multiple fishermen with single hooks and lines at site 1 (gray), and a commercial fisherman with multiple hooks and lines for site 2 (black). Lingcod under the legal limit for total length (<61 cm) were retained by permit at both locations, but were proportionately more abundant among sampled lingcod at site 1, and proportionately more lingcod stomachs were empty at site 2.

The smallest lingcod sampled or observed on a reef was 42 cm TL. Lingcod may be retained by the fishery at 61 cm TL and larger. Although undersized lingcod were sampled by special permit at both sites, the commercially caught samples were biased toward larger lingcod and most of the lingcod sampled were within a relatively narrow size range, likely because the local lingcod population was rebuilding and was dominated demographically by only a few cohorts. Lingcod juveniles settle onto a variety of habitats but were not observed on reefs. This is not surprising because lingcod are periodically cannibalistic, as shown in this and other studies.

Dietary composition

Of the 60 lingcod stomachs sampled at site 1, 12 were empty and 48 contained prey that were aggregated into 10 categories. At site 2, of the 315 lingcod stomachs sampled, 177 were empty and 138 contained the same 10 prey categories plus Pacific sandlance (*Ammodytes hexapterus*) as a major prey item, as well as market squid (*Loligo opalescens*), Pacific lamprey (*Lampetra tridentata*), and northern anchovy (*Engraulis mordax*) as minor items (Table 2). Because both the number of samples and sampling effort was much greater at site 2, it was expected that more prey types were found in lingcod from there (see Bock, 1987). There were proportionately fewer empty stomachs among captured lingcod, and lingcod were smaller on average at site 1 than at site 2 (Fig. 2). Among prey categories common to both sites, there were significantly more Pacific herring (*Clupea pallasii*) consumed by lingcod sampled at site 1 than at site 2 (two-sided t-test, P=0.01, df=373). A rank concordance test was significant, indicating that prey consumption by category did not differ between sites (Kendall's rank concordance test, P<0 .01, n=15, s=2.03) and therefore the data were pooled for the preference analysis.

After sites were pooled, there were 21 identified species aggregated into 14 ecologically similar prey categories. Among the 342 prey items found in 375 stomachs (50.4% of lingcod stomachs were empty) major prey items were Pacific herring, Pacific sandlance, unidentified fishes, two-spotted octopus (*Octopus bimaculatus*), and pandalid shrimps (*Pandalus* spp.). All other prey groups, including rockfishes, each comprised less than five percent of the total gut contents (Fig. 3). A MME for species accumulation indicated that sampling effort was sufficient (S_{max}=14.91; β=17.21). Of the prey items that were measurable to total length, 14 were confirmed to be rockfishes. The largest of those was 28 cm (the only potential adult), and none was estimated to be more than three years old based on published length-at-age curves (Love et al., 2002). Of the identified young-of-year rockfishes, five were of the "black-spot" group and one was a stripetail (*S. saxicola*). Nearly all rockfishes identified to species were *S. melanops* and less than two years old as inferred by length (Love et al., 2002).

Table 2

Prey found in stomachs of 375 lingcod (*Ophiodon elongatus*) collected off Oregon, where n is the number of stomachs containing a particular prey type and n' is the total number of individuals of a particular prey type; $\%F_o$ is the frequency of occurrence, and $\%N$ is the percentage of prey items. The preference rank for each of 14 aggregated prey categories is also provided, where 1=most preferred prey and 14=least preferred prey.

Prey species	n	n'	$\%F_o$	$\%N$	Preference rank
Transient and pelagic fishes					
Lampetra tridentata	1	1	0.27	0.31	8
Engraulis mordax	2	2	0.53	0.62	6
Clupea pallasii	37	109	9.87	33.64	7
Merluccius productus	7	8	1.87	2.47	4
Ammodytes hexapterus	15	49	4	15.12	2
Skates and flatfishes (soft bottom)				3	
Raja spp.	1	1	0.27	0.31	
Hippoglossus stenolepis	1	1	0.27	0.31	
Citharichthys sordidus	3	3	0.8	0.93	
Parophrys vetulus	1	1	0.27	0.31	
Platichthys stellatus	2	2	0.53	0.62	
unidentified flatfishes	5	5	1.33	1.54	
Reef-dwelling fishes					
Rockfishes					13,14
Sebastes melanops	6	6	1.6	1.85	
Sebastes saxicola	1	1	0.27	0.31	
unidentified rockfishes	7	9	1.87	2.78	
Greenlings					12
Hexagrammos decagrammus	3	3	0.8	0.93	11
Ophiodon elongatus	2	2	0.53	0.62	
Unidentified fishes	28	33	7.47	10.19	
Sculpins					10
Hemilepidotus hemilepidotus	3	3	0.8	0.93	
Scorpaenichthys marmoratus	2	2	0.53	0.62	
Unidentified sculpins	9	9	2.4	2.78	
Invertebrates					
Octopus					9
Octopus bimaculatus	26	30	6.93	9.26	
Octopus dofleini	5	5	1.33	1.54	
Loligo opalescens	3	3	0.8	0.93	5
Pandalus spp.	23	27	6.13	8.33	1
Cancer magister	2	6	0.53	1.85	

The dominant prey type was Pacific herring ($\%F$=9.87, $\%N$=33.64), a transient and pelagic species. Other prey types were clustered and far less dominant in the diet (Fig. 4). Among sampling periods, empty stomachs ranged from 8–81% (mean 56% empty, n=10 sampling periods, SE=5.7). Among sampling months, May–October, the presence of consumed prey among lingcod was unpredictable, regardless of the sampling month (ANOVA, $F_{1,9}$=1.77, P=0.22) and consumption of resident prey appeared to be independent of consumption of transient prey (ANOVA, $F_{1,9}$=2.46, P=0.15).

There were 41 unidentified prey items, 33 of which were confirmed not to be rockfishes. Lingcod eat parts of animals they cannot swallow whole by tearing prey apart (e.g., Pacific giant octopus; personal observ.) and are thus not considered gape-limited with respect to prey preference. Larger lingcod consumed larger prey (Fig. 5) but not distinctly different prey types (adjusted coefficient of determination r^2=0.29, one-way ANOVA $F_{1,71}$=30.3, $P < 0.01$, n=72 measurable prey items). Typically, a single prey item (but as many as 17) was found in a stomach containing prey, and among those stomachs containing more than one prey item, as many as four different species were found.

Numerically, 52% of prey were transient and pelagic, 4% were associated with soft-bottom seafloors, 44% were demersal reef-dwelling species, and of the latter, half were invertebrates. The importance of macroinvertebrates among local prey species is different from what was found in previous studies. Sand

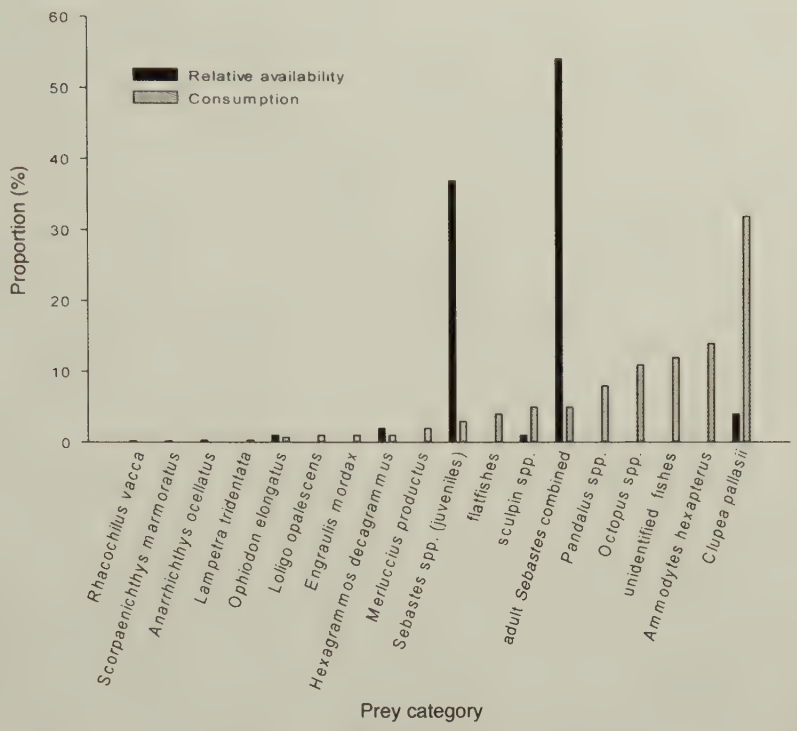

Figure 3

Proportional relative availability (dark bars) of potential prey as determined from nine dive surveys off Oregon for sites 1 and 2 combined, and proportional consumption (light bars) of prey by lingcod (*Ophiodon elongatus*) for sites 1 and 2 combined. The lack of overlap between realized consumption and relative availability indicates that lingcod were not preferentially consuming the most apparently abundant prey types, which were rockfishes (*Sebastes* spp.).

consistently occurred in lingcod stomachs containing both octopus and shrimps, but never with flatfishes of any species. This pattern suggests that these lingcod did not forage for flatfishes directly over the seafloor, but were eating them in the water column. Because lingcod were captured on mid-water lures, they are apparently capable of foraging in the pelagic as well as the benthic zones.

Prey preference

Analysis of identified prey in the pooled data showed that prey selection was not proportional to availability (Johnson's preference, $F_{13,132}$=943, P<<0.001). Rockfishes were significantly "avoided" among prey categories (Waller-Duncan [1969] multiple comparisons, P =0.01, n=145). In order of preference, adult rockfishes were ranked last followed by subadult rockfishes (Fig. 6). Preference ranking also indicated that transient and pelagic prey (Pacific herring and Pacific sandlance) were among the most preferred prey. The January surveys could not be temporally matched with consumption data and therefore were excluded from this analysis, as were empty stomachs. However, because of the inherent temporal and spatial patchiness of transient prey, as well as the difficulty in comparing very different types of prey, it was not possible to differentiate prey preference ranks among Pacific herring, Pacific sandlance, shrimps, and octopus. Other categories fell between these extremes (Fig. 6).

Discussion

These data indicate that lingcod off the coast of Oregon 1) are highly generalized predators of both fish and invertebrates in multiple habitats; 2) select prey disproportionately to prey abundance; and 3) do not differentially target rockfish as prey. Rockfishes may not be preferred because, unlike any other identified prey items, they have robust, venomous spines (Smith and Wheeler, 2006). In this case, experimental manipulation of predator and prey densities at meaningful temporal and spatial scales is not possible. For this reason it is necessary to use consumption and relative density estimates in a static model to find evidence of an effect. If consumption is very low relative to prey abundance, as is the case with predation on rockfishes, then any

direct effects on the population dynamics of either are unlikely to be strong.

There is incomplete spatial and temporal overlap between prey availability and consumption data sets and the variance may be greater than it otherwise would be because the dive surveys are disjunct. Still, the MME beta value and asymptotic curve stability of the combined surveys suggest that the heterogeneity of available prey can be detected with this level of effort and that the data are representative at this spatial and temporal scale. The prey availability data are not intended to reflect regional abundance. When a prey type such as Pacific herring is ranked low with respect to availability relative to rockfishes, it suggests rockfishes have more constant (less patchy) temporal and spatial overlap with lingcod. In this way the potential for encounter is much higher between lingcod and rockfishes.

Large, highly generalized predators eat many different prey types and often do so infrequently, and therefore sample sizes must be relatively large to adequately capture the heterogeneity of the consumption data (e.g., Kingsford, 1992). With 375 samples, the dietary data reported here describe the relative abundance of prey categories in the diet of lingcod over a limited geographical area during half the year. However, Steiner (1979) collected summer and winter stomach samples and did not show an increase in lingcod consumption of rockfishes in winter and the number of samples collected appears to have captured the heterogeneity in the consumption data. The primary sources of error in these data include potential misidentification of prey and undefined rates of egesting stomach contents. Additionally, the digestion rates for free-living lingcod are unknown. Although they do reflect the relative temporal distributions of different prey types, the data from dive surveys were biased by both the spatial and temporal patchiness of transient prey, and by asymmetric sampling accuracy among habitats for prey types that were difficult to observe. However, rockfishes are highly observable and there was clearly a strong negative preference (or avoidance) for rockfishes than for all other prey types. Hydro-acoustic tracking studies of black rockfish have shown they move less than a few hundred meters over periods of months (Parker et al., 2008).

The gape-limitation hypothesis predicts that prey-size selection is consistent with optimal diet theory at the lower bound and the physical constraint of mouth size at the upper bound (Schmitt and Holbrook, 1984) and can be useful for predicting foraging behavior in fish (e.g., Persson et al., 1996). Larger lingcod tend to consume larger prey, but the gape-limitation hypothesis, or size-spectrum hypothesis (Scott and Murdoch, 1983), is not particularly useful for predicting prey selection in these animals because all sizes of lingcod eat small prey and lingcod consume parts of larger prey. Gape-limitation does not effectively predict which prey species or functional groups adult lingcod of different sizes will prefer to consume, nor do these data show a distinct shift to larger prey with increasing lingcod size.

In relatively long-lived generalist predators such as lingcod, dietary sampling at temporal scales over two years may be required for meaningful patterns in consumption to emerge. The variance in consumption by local predators of transient prey is high and may be independent of regional prey abundance. If consumption of resident prey is relatively even over time, the resident prey types may provide a maintenance resource and more ephemeral prey may provide sporadic opportunities for enhanced growth and reproduction. Additionally, indirect effects can be important to the distribution of predators. Besides direct consumption, risk effects (modification of prey distribution or behavior because of a perceived predation risk) may have an important influence on community structure (Creel and Christianson, 2007; Madin et al., 2010).

There is concern that lingcod predation may reduce the efficacy of marine reserves in the recovery of some overfished populations of rockfishes. In a recent study that addressed this issue in Puget Sound, Washington, Beaudreau and Essington (2007) found that in 560 lingcod (<30–108 cm TL) sampled inside and outside marine reserves, 6.8% of the total number of prey items were rockfishes. All individual rockfish identified to species were Puget Sound rockfish (*S. emphaeus*) and 0.4% of all prey were confirmed to be other species of *Sebastes*. The Puget Sound rockfish is a

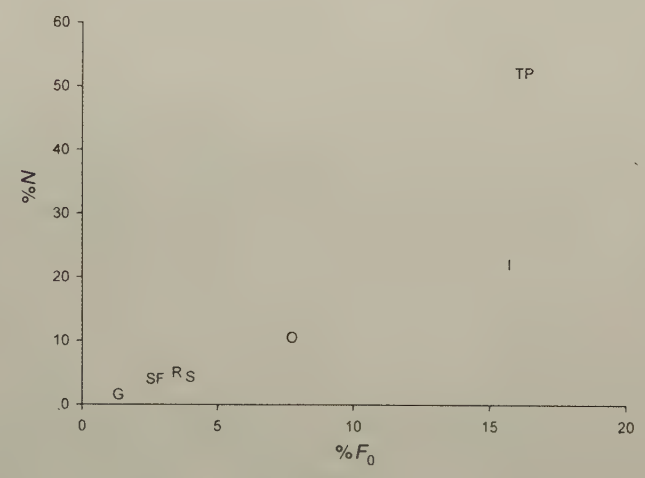

Figure 4

Percentage of lingcod (*Ophiodon elongatus*) prey (*%N*) as a function of frequency of occurrence in the diet ($\%F_o$). Prey categories are as follows: TP=transient-pelagic fishes (predominantly Pacific herring [*Clupea pallasii*]); SF=skates (*Raja* spp.) and flatfishes; S=sculpins (family Cottidae); R=rockfishes (*Sebastes* spp.); G=greenling (family Hexagrammidae)(including cannibalism by lingcod); I= invertebrates; O=other (including uncategorized, unidentified fishes). TP, for example, was both a relatively large percentage of the overall diet, and also commonly occurred as a prey type among lingcod sampled.

very small species that matures in 1–2 years. It is a schooling species and is often found in high densities. It is not fished either recreationally or commercially and thus is not the focus of recovery efforts. The largest measurable rockfish in Beaudreau and Essington's (2007) study was 16.6 cm. Combined with the results from Steiner (1979) and this study, lingcod of any size rarely prey on larger-body rockfishes. Beaudreau and Essington (2007) state that model results suggest intensive lingcod fishing is likely to disproportionately alleviate predation pressure on larger rockfishes. However, combined empirical evidence from this study and the two studies cited immediately above does not support this assertion.

Of all prey items found in this study, only one was a potentially reproductive rockfish and it apparently had been ingested within 24 hours of capture. This ratio simplifies to less than one adult rockfish consumed per adult lingcod per year, whereas the dive surveys revealed an average of 40 adult rockfishes living in the vicinity of each lingcod. If these ratios are representative, they suggest that lingcod predation is not a primary source of mortality for nearshore adult rockfishes off the coast of Oregon. Nor do lingcod appear to be a primary source of mortality of juvenile or young-of-the-year rockfishes because they were only slightly more likely than adult rockfishes to be eaten by lingcod. Hobson et al. (2001) found predation by black rockfish, blue rockfish, and kelp greenling was the primary source of mortality for postsettlement juvenile rockfishes in northern California.

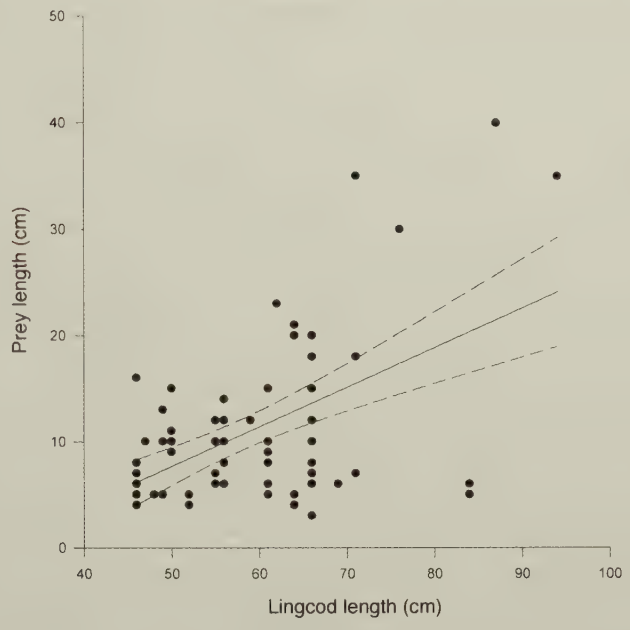

Figure 5

Lingcod (*Ophiodon elongatus*) total length (cm) versus prey length for each of 73 measurable prey items. The largest prey item was a Pacific giant octopus (*Octopus dofleini*) estimated at 70 cm in length that two individual lingcod, 72 cm and 93 cm respectively, appeared to have each eaten half. This prey item is represented by two data points, each with an assigned prey length value of 35 cm. The slope of the regression line (adj. R^2=0.29) is influenced by the three largest prey items. Dashed lines represent the 95% confidence interval.

Conclusions

The results of this study show that lingcod are highly generalized predators that consume a broad variety of prey in terms of taxa, body form, and habitat. Lingcod are mobile, opportunistic, ambush predators that do not appear to be individually specialized. On the basis of the number of empty stomachs, they frequently go at least several days without eating, indicating there may be large differences between local prey abundance and prey availability (see Menge, 1972; Kelly, 1996). Better information is required on foraging range in relation to differences in habitat and prey availability to better understand lingcod foraging behavior as it relates to prey density. Nevertheless, this study strongly indicates that lingcod do not pose a threat to rockfish populations.

EBFM requires more information than single-species management approaches. In data poor systems, and particularly those that are difficult to access, higher echelon data describing interactions among both targeted and nontargeted species will be very difficult to develop. However, this study shows that untested assumptions about trophic relationships may lead to counterproductive management decisions, particularly with respect to large predatory species (Baum and Worm, 2009). Marine reserves can be an effective management tool for the conservation and recovery of exploited and other species, and particularly so where species of particular interest have relatively site-attached adult populations. In these cases trophic relationships, especially among resident and transient species, are a critical uncertainty and these relationships can only be fully understood through both consumption and relative prey availability measures. In this case, a preference index provides much more information about the likely result of fluctuations in predator and prey populations than would be the case with diet data alone.

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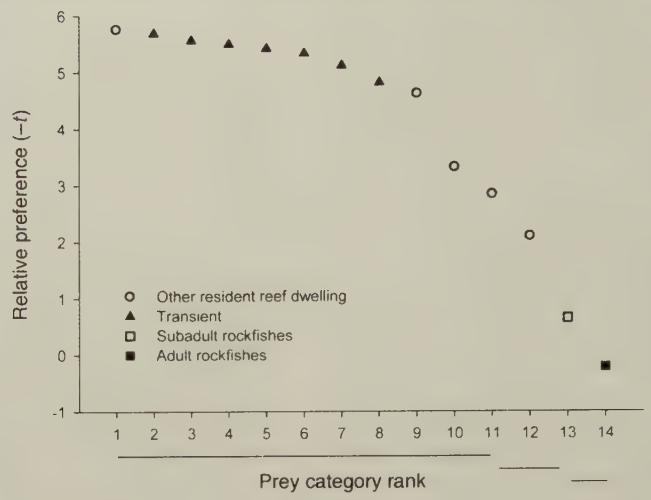

Figure 6

Mean relative prey "preference" (Johnson's [1980] – t) of 186 lingcod (*Ophiodon elongatus*) captured at two sites off Oregon containing prey from 14 prey categories, listed from most preferred (rank 1) to least preferred (rank 14). Values with the same underline are not significantly different (P>0.05, Waller-Duncan multiple comparison). Rank numbers identify prey categories as listed in Table 1. Both juvenile and adult rockfishes (*Sebastes* spp.) were significantly avoided as prey types in comparison with all other prey groups.

for help with Figure 1; three anonymous reviewers; and Captain J. W. Cheesman (1962–2011).

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Variations in eastern North Pacific demersal fish biomass based on the U.S. west coast groundfish bottom trawl survey (2003–2010)

Aimee A. Keller (contact author)
John R. Wallace
Beth H. Horness
Owen S. Hamel
Ian J. Stewart

Email address for contact author: aimee.keller@noaa.gov

National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Northwest Fisheries Science Center
Fishery Resource Analysis and Monitoring Division
2725 Montlake Blvd. E.
Seattle, Washington 98112

Abstract—In response to declining biomass of Northeast Pacific groundfish in the late 1990s and to improve the scientific basis for management of the fishery, the Northwest Fisheries Science Center standardized and enhanced their annual bottom trawl survey in 2003. The survey was expanded to include the entire area along the U.S. west coast at depths of 55–1280 m. Coast-wide biomass and species richness significantly decreased during the first eight years (2003–10) of this fishery-independent survey. We observed an overall tendency toward declining biomass for 62 dominant taxa combined (fishery target and nontarget species) and four of seven subgroups (including cartilaginous fish, flatfishes, shelf rockfishes, and other shelf species), despite increasing or variable biomass trends in individual species. These decreases occurred during a period of reduced catch for groundfish along the shelf and upper slope regions relative to historical rates. We used information from multiple stock assessments to aggregate species into three groups: 1) with strong recruitment, 2) without strong recruitment in 1999, and 3) with unknown recruitment level. For each group, we evaluated whether declining biomass was primarily related to depletion (using year as a proxy) or environmental factors (i.e., variation in the Pacific Decadal Oscillation). According to Akaike's information criterion, changes in aggregate biomass for species with strong recruitment were more closely related to year, whereas those with no strong recruitment were more closely related to climate. The significant decline in biomass for species without strong recruitment confirms that factors other than depletion of the exceptional 1999 year class may be responsible for the observed decrease in biomass along the U.S. west coast.

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Over the past 20 years, a number of changes have occurred in the Northeast Pacific groundfish fishery with low abundance observed for multiple species (Field and Fox, 2006; Levins et al., 2006). Historically catch and annual exploitation rates increased from the 1950s through the 1980s and then declined rapidly. Between 1999 and 2002, nine important fish stocks in the eastern North Pacific off the U.S. west coast were declared overfished, at which time the Pacific Fishery Management Council (PFMC) introduced a series of regulatory measures to reduce fishing pressure. Management actions included reducing total allowable catch and fleet size, and closure of large areas of the upper continental shelf to fishing (PFMC, 2008a). In response to management concerns the NOAA Northwest Fisheries Science Center (NWFSC) also expanded and standardized the annual west coast groundfish bottom trawl survey to provide enhanced scientific information for managers. Since 2003, the Northwest Fisheries Science Center (NWFSC) has conducted a comprehensive fishery-independent bottom trawl survey covering the entire coast from the U.S.–Canada to the U.S.–Mexico borders, at depths of 55 to 1280 m (Keller et al., 2008). This groundfish survey follows strict sampling protocols with standardization of vessels, fishing gear, deployment methods, catch sampling practices, and geographic extent from 2003 onward (Stauffer, 2004).

Here we summarize variations in biomass indices for species collected during the 2003–10 fisheries-independent west coast groundfish bottom trawl survey. We evaluate if an observed decline in biomass of demersal fish (target and nontarget species) from 2003 through 2010 can be attributed primarily to recruitment (i.e., depletion after strong recruitment events for multiple species in the late 1990s) or to climate variability (i.e., poor environmental conditions).

The 2003–10 survey time series covers a period within the California Current system characterized by 1) reduced catch and exploitation of groundfish species relative to historical rates (Worm et al., 2009; Hilborn et al., in press); 2) the population effects of a very strong 1998–99 year class observed for many west coast groundfish species (e.g., Pacific hake [*Merluccius productus*], English sole [*Parophrys vetulus*], http://www.pcouncil.org/, accessed June 2011); and 3) a phase shift in the Pacific Decadal Oscillation (PDO), an El Niño-like pattern of Pacific climate variability linked to productivity (Mantua et al., 1997). The PDO is detected as warm or cool surface waters in the western Pacific Ocean, north of 20°N, that shift phases on a scale of about

10 to 30 years. During a "warm" or "positive" phase, part of the eastern Pacific Ocean warms and productivity of waters off the U.S. west coast declines; during a "cool" or "negative" phase, the opposite pattern occurs (Schwing et al., 2009).

The aim of this study was to evaluate the importance of depletion after strong recruitment versus environmental effects on declining biomass observed during groundfish surveys in the western U.S. shelf system. We used data from 24 stock assessments conducted since 2005 (http://www.pcouncil.org/, accessed September 2011). With information contained in the assessments we separated 62 dominant species into three groups: those with strong recruitment during the late 1990s–early 2000s, those without a strong recruitment during this period, and those with unknown year-class strength. For each group and the overall biomass indices for all groups we evaluated regression models between demersal fish biomass (2003 through 2010) along the U.S. west coast versus year (as a proxy for gradual depletion after recruitment of exceptional year classes to the fishery) and the PDO index, an ecosystem-level indicator of climate variability. For each comparison, the most appropriate model for describing the relationship with biomass was determined. A similar analysis was undertaken for species richness. We additionally present information on frequency of occurrence (number of positive hauls) and depth distribution by species.

Materials and methods

Survey design and methods

The NWFSC conducted annual bottom trawl surveys of groundfish resources off the U.S. West Coast using standardized procedures from 2003 through 2010 (Keller et al., 2008). Surveys occurred May through October from the area off Cape Flattery, Washington (lat. 48°10′N), to the U.S.–Mexico border (lat. 32°30′N) at depths of 55–1280 m (Fig. 1). The entire geographic extent of the survey was covered twice each year by two west coast commercial fishing vessels (20 to 28 m in length) per pass. Each year sampling extended from late May through late July for the first period and mid-August through late October for the second. A stratified random sampling design was used, in which the surveyed region was subdivided into ~13,000 cells of equal area (1.5 nmi longitude by 2.0 nmi latitude) (Fig. 1). An average of 700 primary cells was randomly selected each year, stratified by geographic location and depth. The geographic allocation was based on a simple north–south division at 34°30′N lat. (Point Conception, California) with 80% of the effort in the northern portion of the survey and 20% in the southern range. The survey area was further stratified into depth zones as follows: north of Point Conception, 40% of the cells were in the shallow depth zone (55–183 m), 30% at mid-depths (184–549 m), and 30% in the deep stratum (550–1280 m); and south of Point Conception, 25% were in the shallow depth zone, 45% at mid-depth, and 30% in the deep stratum. Four chartered west coast fishing vessels were assigned an equal portion of stations to sample per year except in 2004 when only three vessels were used.

Vessels were equipped with customized Aberdeen-style nets with a small mesh (3.8 cm stretched measure) liner in the codend, a 25.9-m headrope, and a 31.7-m foot rope. All fishing operations were conducted in strict compliance with national and regional protocols detailed in Stauffer (2004). Simrad Integrated Trawl Instrumentation (ITI , Kongsberg Simrad Mesotech Ltd., Port Coquitlam, B.C., Canada[1]) was used to monitor and record net performance and position for each haul. A differential global positioning system (DGPS) navigation unit (Northstar 500, Northstar Technologies, Acton, MA) was used to monitor towing speed during each haul. Standard survey haul positions were estimated from DGPS data—generally the mid-point between the net touchdown and net liftoff positions. Average net speed over ground and distance fished were calculated from the position data for the trawl and actual bottom time (Keller et al., 2008).

Samples were collected by trawling within the randomly selected cells (Fig. 1) for a target fishing time of 15 minutes at a target speed of 1.13 m sec^{-1} (2.2 knots). All fish and invertebrates were sorted to species (or the lowest possible taxon), and then weighed by using an electronic, motion-compensated scale (Marel, Reykjavik, Iceland). Abundance was not analyzed in this study because not all individuals were counted. Total abundance is estimated from biomass and the two cannot be considered independent without analysis of the variability of mean weights. That analysis is beyond the scope of the present study. Near bottom temperature (°C) and depth (m) were measured during each trawl with an SBE 39 temperature and pressure recorder (Sea-Bird Electronics, Inc., Bellevue, WA) attached to the head rope. Mean tow depths were computed as the average of all depth recordings from the center 80% of the trawl duration (net touch down to lift off). Only tows judged to be acceptable (based on postcollection analysis of bottom contact, net performance, and other metrics; Stauffer, 2004) were included in the data analyses.

Analyses of catch

To limit this analysis to the most reliably sampled species, we initially examined catch for 310 individual fish species summed over the 2003–10 period. When graphed by species in order of descending catch, no obvious break was apparent and therefore we included all demersal species with an overall catch greater than 450 kg. This break point included the 62 most abundant species in the survey and incorporated 45 of the demersal groundfish species present in the Pacific Fishery Management Council Pacific Coast groundfish

[1] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

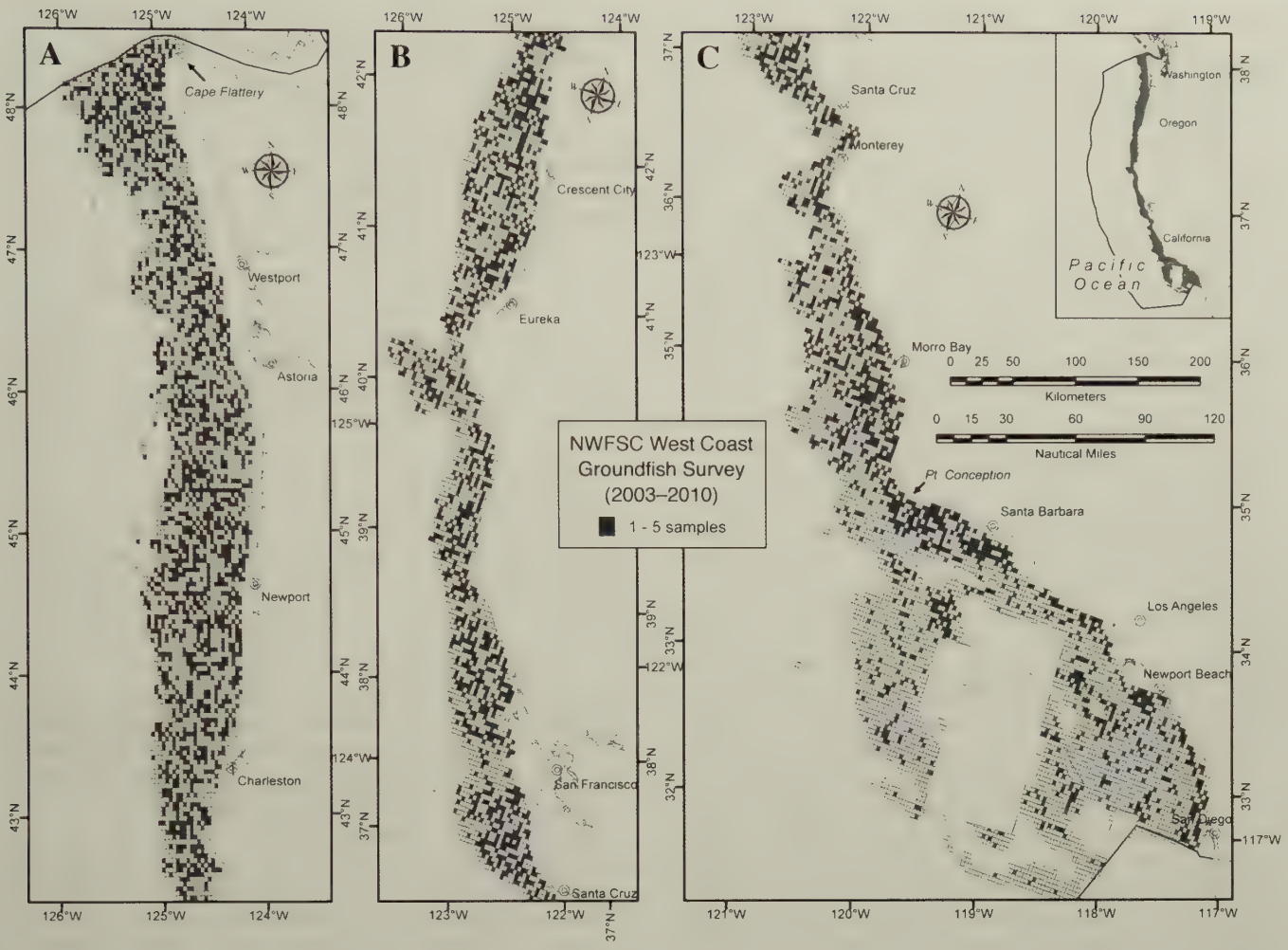

Figure 1

Geographical extent of the Northwest Fisheries Science Center's West Coast Groundfish Bottom Trawl Survey and the location of stations (shaded) trawled one to five times from 2003 through 2010. (**A**) Stations off Washington and Oregon. (**B**) Stations off northern California. (**C**) Southern California stations. The Cowcod (*Sebastes levis*) Conservation Area in Southern California was excluded from the experimental design because it is closed to fishing for groundfish species.

fishery management plan (PFMC, 2008b), as well as two important benthic invertebrates and 15 non-fished species. The break point also represented a greater than 10% difference in catch relative to the next most abundant species. Species-specific catch per unit of effort (CPUE, kg ha^{-1}) was calculated for each tow on the basis of area swept. Area swept was computed from the mean net width for each tow multiplied by the distance fished. Mean CPUE was calculated for each stratum (depth and geographic region, including those with zero catch), by species. Species-specific biomass indices (b, in metric tons [t]) were computed by multiplying the mean CPUE by the appropriate stratum area and then summing the strata biomasses. The estimate of the variance of the biomass was the sum of the variances of the strata involved:

$$Var(\tilde{b}) = \sum_{i=1}^{n} \left(Var(\overline{CPUE}_i) \times A_i^2 \right),$$

with n equal to the number of strata, and A equal to the area of each stratum (km^2). Standard errors (SE) for the annual species-specific biomass indices were calculated using standard statistical techniques (Cochran, 1977).

To examine variation in biomass over time, species groups were initially designated on the basis of either taxonomy or depth (e.g., shelf and slope rockfishes). Subsequently we examined relationships between biomass and both year and the PDO index using groups designated by the presence, absence, or unknown occurrence of a strong recruitment during the mid to late 1990s and early 2000s. In all cases biomass was summed over the appropriate group and variance was calculated as previously described. For those species included in the 2003–10 biomass analyses, we also calculated mean depth (m) by averaging station values weighted by catch for each species in each year (Hsieh et al., 2008).

Recruitment versus PDO indices

Stock assessments for 24 of the 62 species in the analyses have been published by the PFMC since 2005 (available at http://www.pcouncil.org/groundfish/stock-assessments/safe-documents/2011-safe-document/, accessed September 2011) and provide information on the number of recruits by year. We examined stock assessments for each species to determine whether strong recruitment events occurred during the period from the mid to late 1990s through 2002. Annual recruitment strength is generally modeled in the assessments as random deviations about a stock-recruitment (S-R) relationship. These deviations and the central tendency of the S-R curve are informed by all other sources of available information (i.e., observed lengths, weights, age, and trend information from fishery-dependent and independent sources) and will reflect predation intensity, climate, and other influences (Methot, 2011). For this analysis, we defined strong recruitment as 1.7–5 times greater than the average recruitment during the 10 to 14 years before the most recent assessment.

We subsequently subdivided the 62 species included in our study into three groups: those with strong recruitment during the late 1990s, those without strong recruitment during this period, and those with unknown recruitment levels. We summed the biomass indices for all species within each group and the overall biomass indices for all three groups and regressed these summed values versus year. We reasoned that declining biomass indices would be more tightly tied to time for those species with elevated recruitment as the resulting exceptionally strong cohorts declined due to natural and fishing-induced mortality in the early 2000s.

Biomass indices for the aggregated subgroups and overall were also compared with the PDO, a widely used index of climate variability for the California Current system. The PDO is an index based on patterns of variation in sea surface temperature of the North Pacific from 1900 to the present (Mantua et al., 1997; Schwing et al., 2009). Although derived from sea surface temperature data, the PDO index is well correlated with other environment factors, including sea level pressure, winter air temperature, wind shear, and precipitation, as well as other Pacific climate indices (ENSO [El Niño-Southern Oscillation] and MEI [multivariate ENSO index]). For comparison with the annual survey data, monthly PDO values were averaged annually (November to October) to include the survey period each year (Mantua[2]).

Species richness

Coast-wide estimates of species richness were calculated as area-weighted mean number of fish species taken per trawl sample. Estimates were stratified by survey year (2003–10), depth (55–183 m, 184–549 m, and 550–1280 m), and geographic region (one degree latitudinal increments from 32° to 49°N) for all fish species. Estimates were built upon the number of distinct fish species reported for each trawl sample. Mean species counts were determined for each stratum and weighted by the proportion of stratum area within the total area. Annual species richness estimates were computed as the sum of these area-weighted species counts within the area of interest (per depth range or coast-wide) and survey year. Species richness variance within each area was similarly estimated as the sum of stratum variances weighted by their associated squared proportion of stratum area within the total area. Standard errors of the mean were computed as the square root of the ratio of the variance estimate to the stratum count for each area (i.e., within a specific depth stratum or coast-wide). We compared species richness over time by regressing against year and also evaluated the relationship between species richness and the annual Pacific Decadal Oscillation (PDO) index. In both cases, regression analyses by depth strata and overall depth were undertaken

Statistical analyses

For the biomass data we examined individual species, and present for comparison several aggregate groups formed by summing species coast-wide biomass indices (metric tons, t). For each species, regression analysis was used to initially investigate the relationship between annual biomass indices and year. To account for the large number of tests conducted, a sequential Bonferroni correction with a significance level of 0.05 was applied to the data (Peres-Neto, 1999). Grouping data for later analyses (initially by depth or taxonomic group to examine trends over time for aggregated data and subsequently by the presence, absence, or unknown occurrence of exceptionally large year classes after recruitment) resulted in fewer tests and no Bonferroni correction was applied. Results for biomass and species richness were statistically compared with year and the PDO index by linear and multiple regression (GLM) by using SAS for Windows (SAS Institute, Inc., Cary, North Carolina). To stabilize the variance, the natural logarithm of the response variable was used in the regression models; however, even after the transformation, annual variance estimates were highly variable for some species. Regressions weighted by the variance estimate of the annual values were therefore used to examine interactions between annual biomass indices and species richness versus year, PDO values, or both (Draper and Smith, 1981).

The Akaike information criterion (AIC) was used to choose between competing models (i.e., recruitment, environmental variability or both) when comparing biomass values, summed by groups, versus year and the PDO index (Sakamoto et al., 1986). For each group, the best model was selected on the basis of the smallest AIC value (AIC_{min}). A similar comparison was done between species richness versus year, the PDO index, and both year and the PDO index. To determine whether a model

[2] Mantua, N. 2010. Personal commun. Dep. Atmospheric Sciences, Univ. Washington, Seattle, WA 98195.

other than the best model was plausible, the difference in AIC values for each model was calculated as

$$\Delta_i = AIC_i - AIC_{min}.$$

Models with $\Delta_i < 2$ are considered equivalent to the best model (AIC_{min}) and candidate models with $\Delta_i > 10$ are highly unlikely to be plausible alternatives for the best model. Candidate models with Δ_i between 3 and 7 have less support than the best model (Burnham and Anderson, 2002).

Results

Biomass

Between 2003 and 2010, 5271 trawls were successfully conducted as part of the groundfish survey with an annual average of 659 trawls yr^{-1} (range: 505 to 722 trawls; Fig. 1). Although an average of 265 individual fish taxa were identified each year (range: 252– 310), the 60 demersal fishes and two benthic invertebrates included in this analysis comprised greater than 99% of the total catch. Annual biomass indices (t) for the 62 individual species revealed variable trends over time (2003–10) (Figs. 2 and 3). Six species exhibited significant ($P<0.001$) increases in biomass indices over time (Fig. 2A), 20 species displayed significant ($P<0.05$) or near significant ($P<0.10$) negative trends (Fig. 3, California skate [*Raja inornata*] and pygmy rockfish [*Sebastes wilsoni*] not shown), and 36 species exhibited nonsignificant trends over time. Representative examples for species with no significant trends are shown for the most abundant species within each group (Fig. 2B). Regardless of trends, both target and nontarget species occurred in each group.

Mean, minimum, and maximum depth (m), and total numbers of positive hauls over the eight year study are shown for the 62 individual species included in the analyses (Table 1). Catch for these 62 species was initially partitioned into seven groups based on taxonomy and depth (in order of decreasing biomass): flatfish (30%), other shallow to mid-depth species (20%), shelf rockfish (15%), sharks, skates, and ratfish (13%), other deep water species (9%), thornyheads (8%), and slope rockfish (5%), to examine trends over time. The weighted mean depths for shallow to mid-depth species was <500 m, and the weighted average for deep water species was >650 m. Shelf rockfish occurred at average depths ranging from 101 to 209 m, whereas slope rockfish were somewhat deeper (226–456 m). In general, rockfish were encountered in fewer hauls than other subgroups.

Despite variations in biomass indices at the species level, four of the seven groups initially examined here (with the exception of slope rockfish, thornyheads, and other deep water species) and overall biomass indices decreased significantly ($P<0.05$) over time (Fig. 4). Overall aggregate coastwide biomass indices for all 62 species decreased approximately 60% from 2,308,207 t in 2003 to 1,384,391 t in 2010. However the lowest biomass (1,373,473 t) was recorded in 2008 (the year of the lowest PDO and also possibly a good recruitment year) followed by slight increases in 2009 and 2010.

Recruitment versus PDO indices

Our initial analyses based on biomass indices for species grouped taxonomically or by depth indicated that deepwater species, such as thornyheads and slope rockfish, did not significantly decrease over time (Fig. 4). However because some species within these groups either decreased significantly or displayed decreasing trends (Figs. 2 and 3), we included all 62 species when we separated demersal catch into categories based on recruitment. Our examination of 24 stock assessment models revealed that 13 species had large recruitment events occurring primarily in 1999 (arrowtooth flounder [*Atheresthes stomias*], English sole, Pacific hake, sablefish [*Anoplopoma fimbria*], bocaccio [*Sebastes paucispinis*], chilipepper rockfish [*Sebastes goodie*], splitnose rockfish [*Sebastes diploproa*], but occasionally somewhat earlier (petrale sole [*Eopsetta jordani*], longspine thornyhead [*Sebastolobus altivelis*]), or later (Dover sole [*Microstomus pacificus*], greenstriped rockfish [*Sebastes elongates*], darkblotched rockfish [*Sebastes crameri*], Pacific ocean perch [*Sebastes alutus*]). Eleven additional species assessed since 2005 did not display significantly larger individual recruitment levels during the period examined (spiny dogfish [*Squalus acanthias*], longnose skate [*Raja rhina*], lingcod [*Ophiodon elongatus*], blackgill rockfish [*Sebastes melanostomus*], canary rockfish [*Sebastes pinniger*], greenspotted rockfish [*Sebastes chlorostictus*], shortbelly rockfish [*Sebastes jordani*], widow rockfish [*Sebastes entomelas*] yelloweye rockfish [*Sebastes ruberrimus*], yellowtail rockfish [*Sebastes flavidus*], shortspine thornyheads [*Sebastolobus alascanus*]). Stock assessments have not yet been conducted on the remaining 38 species included in our analyses.

During the 1999–2010 period, when depletion of a strong year class by fisheries was expected to result in declining biomass trends, we observed variable trends in the PDO index (Fig. 5). Changes in the PDO index from 1999 to 2010 indicate that average climate in the California Current system gradually shifted from cool (1999–2001) to warm (2003–06) and back to cool (2007–10) conditions (Fig. 5). We summed biomass for each of the three groups previously described and overall (all species combined) and regressed aggregate biomass (natural log transformed) versus year and annual PDO indices (Fig. 6). We noted significant ($P<0.001$) or near-significant ($P=0.06$) inverse relationships for all groups and overall versus year (Fig. 6). For species with strong recruitment events in 1999, the trend in biomass over time was increasingly downward, whereas for those with no or unknown recruitment there was a tendency for biomass to increase in recent years (Fig. 6). All groups also demonstrated significant relationships with the annual PDO indices (Fig. 6); however, the greatest

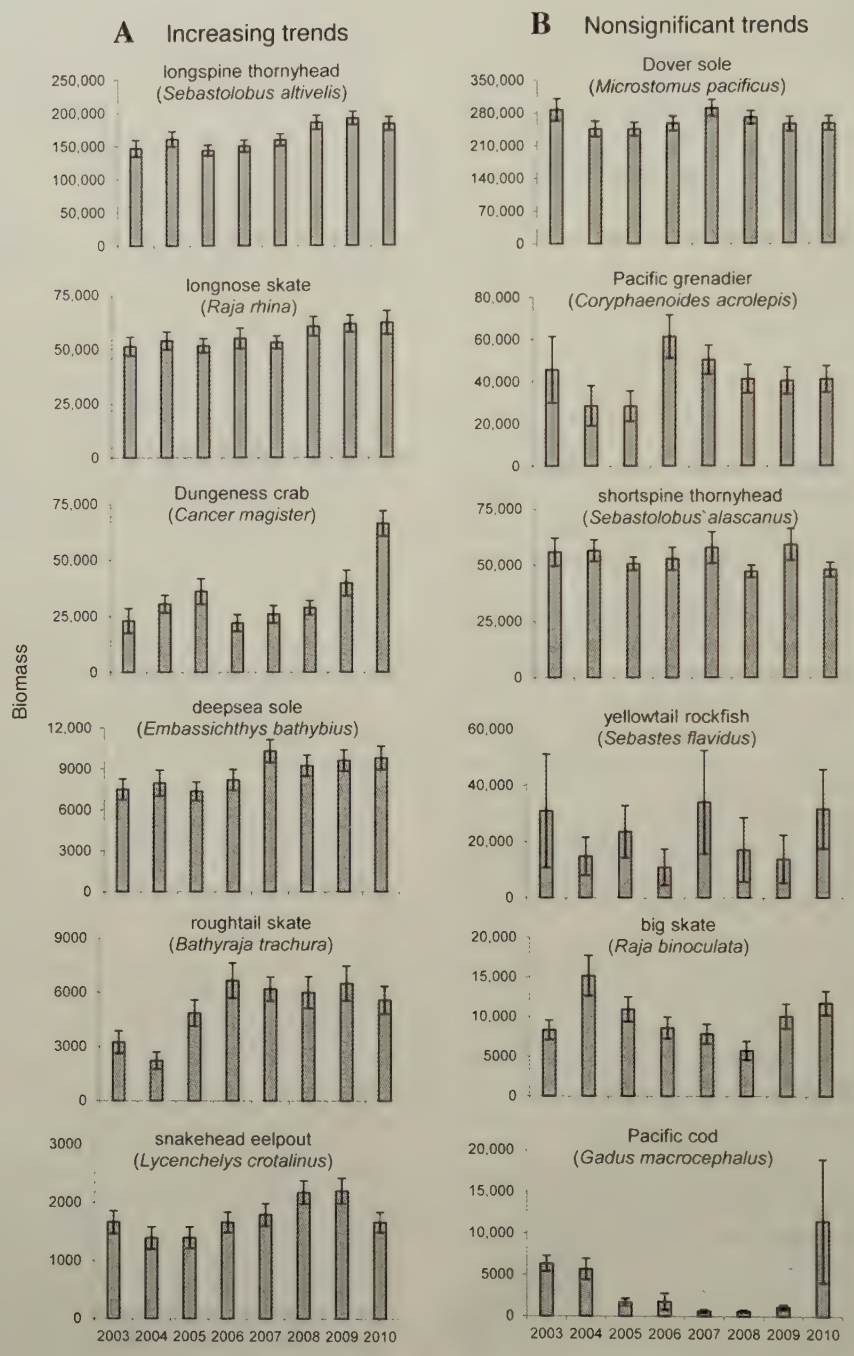

Figure 2

(**A**) Increasing and (**B**) nonsignificant trends in annual, coast-wide demersal biomass indices (in metric tons, t) for 12 taxa caught in the Northwest Fisheries Science Center's West Coast Groundfish Bottom Trawl Survey, 2003–10. Taxa are ranked from highest (top) to lowest (bottom) biomass for each category, and standard errors are shown. All six species exhibiting significant ($P<0.05$) or near-significant ($P<0.10$) increases in biomass indices over time are shown; however representative examples of species with nonsignificant trends (36 species) are shown only for the most abundant taxa for each subgroup described in Table 1.

Figure 3

Decreasing trends in demersal biomass indices in metric tons (t) (±standard error) for 18 of 20 taxa caught in the Northwest Fisheries Science Center's West Coast Groundfish Bottom Trawl Survey, 2003–10. With the exception of California skate and pygmy rockfish, all species exhibiting significant ($P<0.05$) or near-significant ($P<0.10$) decreases in biomass indices over time are shown.

amount of variation in biomass was explained by the PDO indices for those species with no strong recruitment during the late 1990s. We used AIC to determine which model (i.e., based on year, PDO indices or combined) provided the best fit to the data for each group (Table 2). For species with strong recruitment, the regression of biomass versus year had the minimum AIC value; for species without strong recruitment the model incorporating PDO indices provided the best fit. For both other groups (unknown recruitment and overall),

Table 1

Common name, scientific name, and group designations according to taxonomy or depth for 62 dominant demersal species collected during the 2003 to 2010 Northwest Fisheries Science Center West Coast Groundfish Bottom Trawl Surveys. Mean, minimum, and maximum depth, and the total number of positive hauls per species are shown for the 2003 to 2010 period. Mean values are weighted by catch per unit of effort to accurately reflect average depth.

Common name	Scientific name	Depth (m)			Hauls (No. of hauls)
		mean	min.	max.	
Sharks, skates, ratfish					
big skate	*Raja binoculata*	104	56	332	668
California skate	*Raja inornata*	107	56	792	517
filetail cat shark	*Parmaturus xaniurus*	489	113	1224	472
longnose skate	*Raja rhina*	265	57	1227	2934
sandpaper skate	*Bathyraja kincaidii*	284	59	1173	1631
spiny dogfish	*Squalus acanthias*	171	57	1143	1737
spotted ratfish	*Hydrolagus colliei*	185	56	1241	2521
Flatfish					
arrowtooth flounder	*Atheresthes stomias*	208	58	992	1726
curlfin sole	*Pleuronichthys decurrens*	94	56	440	473
Dover sole	*Microstomus pacificus*	382	56	1246	4205
English sole	*Parophrys vetulus*	130	56	480	1957
flathead sole	*Hippoglossoides elassodon*	146	62	346	332
Pacific sanddab	*Citharichthys sordidus*	107	56	491	1554
petrale sole	*Eopsetta jordani*	136	56	541	2059
rex sole	*Glyptocephalus zachirus*	235	56	937	3147
slender sole	*Lyopsetta exilis*	209	57	830	2564
Shallow to mid-depth water (<500 m)					
bigfin eelpout	*Lycodes cortezianus*	343	57	1095	1418
black eelpout	*Lycodes diapterus*	470	82	1143	896
Dungeness crab	*Cancer magister*	139	56	835	1633
lingcod	*Ophiodon elongatus*	137	56	417	1553
Pacific cod	*Gadus macrocephalus*	133	56	285	273
Pacific hake	*Merluccius productus*	281	56	1213	2775
plainfin midshipman	*Porichthys notatus*	109	56	464	656
sablefish	*Anoplopoma fimbria*	495	57	1268	3320
white croaker	*Genyonemus lineatus*	85	56	181	302
Rockfish—shelf					
bocaccio	*Sebastes paucispinis*	159	56	333	263
canary rockfish	*Sebastes pinniger*	139	57	264	340
chilipepper	*Sebastes goodei*	167	56	464	656
greenspotted rockfish	*Sebastes chlorostictus*	146	62	348	303
greenstriped rockfish	*Sebastes elongatus*	156	64	474	1299
halfbanded rockfish	*Sebastes semicinctus*	115	57	440	378
pygmy rockfish	*Sebastes wilsoni*	138	64	268	95
redstripe rockfish	*Sebastes proriger*	158	66	271	120
rosethorn rockfish	*Sebastes helvomaculatus*	207	65	447	420
sharpchin rockfish	*Sebastes zacentrus*	209	76	455	307
shortbelly rockfish	*Sebastes jordani*	170	71	406	405
squarespot rockfish	*Sebastes hopkinsi*	101	59	203	80
stripetail rockfish	*Sebastes saxicola*	175	59	436	1076
swordspine rockfish	*Sebastes ensifer*	156	100	236	30
widow rockfish	*Sebastes entomelas*	195	64	399	182
yelloweye rockfish	*Sebastes ruberrimus*	149	66	250	107
yellowtail rockfish	*Sebastes flavidus*	141	60	343	315

continued

Table 1 (continued)

Common name	Scientific name	Depth (m) mean	Depth (m) min.	Depth (m) max.	Hauls (No. of hauls)
Rockfish—slope					
aurora rockfish	*Sebastes aurora*	456	129	814	689
bank rockfish	*Sebastes rufus*	267	101	499	91
blackgill rockfish	*Sebastes melanostomus*	406	133	647	264
darkblotched rockfish	*Sebastes crameri*	226	84	538	920
Pacific ocean perch	*Sebastes alutus*	279	87	715	344
redbanded rockfish	*Sebastes babcocki*	269	84	550	398
rougheye rockfish	*Sebastes aleutianus*	291	124	798	253
splitnose rockfish	*Sebastes diploproa*	287	68	559	1107
Thornyhead rockfish					
longspine thornyhead	*Sebastolobus altivelis*	767	104	1271	1844
shortspine thornyhead	*Sebastolobus alascanus*	611	67	1268	2590
Deep (>650 m)					
brown cat shark	*Apristurus brunneus*	672	82	1241	1717
California slickhead	*Alepocephalus tenebrosus*	909	477	1268	1097
deepsea sole	*Embassichthys bathybius*	874	276	1271	1116
giant grenadier	*Albatrossia pectoralis*	943	443	1271	838
grooved Tanner crab	*Chionoecetes tanneri*	782	64	1271	1431
Pacific flatnose	*Antimora microlepis*	931	262	1271	890
Pacific grenadier	*Coryphaenoides acrolepis*	915	313	1271	994
roughtail skate	*Bathyraja trachura*	941	107	1271	622
snakehead eelpout	*Lycenchelys crotalinus*	893	63	1264	783
twoline eelpout	*Bothrocara brunneum*	861	343	1271	898

Table 2

Akaike information criterion (AIC), P, coefficient of determination (r^2), and Δ_i for different models fitting annual biomass indices versus year, Pacific Decadal Oscillation (PDO) values, and both variables for three subgroups of demersal species determined by the occurrence of strong recruitment during the late 1990s (with recruitment: n=13, without recruitment: n=11, and unknown: n=38) and overall (n=62). The best model for each group is determined by the minimum AIC value ([1]) within each category, with lower AIC values indicating a better fit. Additionally, when Δ_i values are ≤7 ([2]) there is some support for the alternative model. Similar results are shown for species richness subdivided by depth strata (shallow 55–183 m; mid-depth 184–549 m; deep 550–1280 m and overall 55–1280 m).

	With year			With PDO			With year and PDO			
Models:	AIC	P	r^2	AIC	P	r^2	AIC	P	r^2	Δ_i
Biomass										
with recruitment	−8.9[1]	0.007	0.87	−4.8	0.02	0.62	−1.7	0.008	0.93	7.2
without recruitment	2.8	0.002	0.81	−0.6[1]	0.001	0.84	5.6	0.01	0.91	6.2[2]
unknown recruitment	0.8	0.07	0.45	−5.1	0.01	0.70	−8.7[1]	0.0002	0.99	9.5
all	−6.3	0.001	0.85	−7.5	0.002	0.81	−11.9[1]	0.0001	0.99	5.6[2]
Richness										
shallow	23.1	0.15	0.34	15.7[1]	0.009	0.71	18.4	0.10	0.75	7.4
mid-depth	17.5	0.06	0.49	12.6[1]	0.01	0.68	16.1	0.12	0.73	4.9[2]
deep	18.7	0.28	0.19	16.0	0.20	0.20	12.8[1]	0.05	0.84	5.9[2]
all	15.9	0.08	0.45	7.6[1]	0.004	0.80	13.4	0.08	0.79	8.3

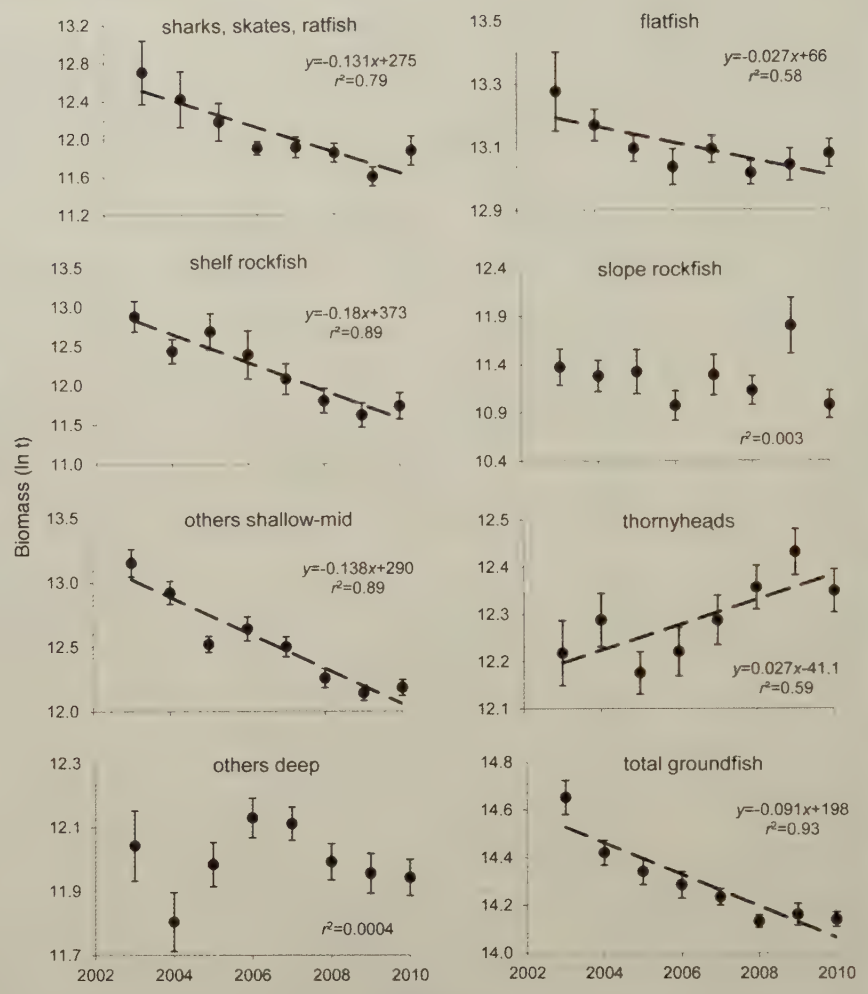

Figure 4

Expanded coast-wide biomass indices (expressed as the natural log in metric tons, [t]) and standard errors as a function of time (year) for 62 dominant demersal taxa collected during the 2003–10 groundfish survey, subdivided into seven subgroups (Table 1), and summed overall. Regression equations for subgroups with significant decreasing trends ($P<0.05$) over time and coefficients of determination (r^2) are displayed.

the minimum AIC value occurred for models incorporating both year and PDO indices combined (Table 2). The Δ_i for the four biomass models indicate that none of the models are equivalent to the best model; however, the observed $\Delta_i \leq 7$ for two of the four groups suggest some support for alternative models (Table 2).

Species richness

Species richness indices incorporated all fish collected during the 2003–10 surveys, including rare deep-water species and those not normally associated with the bottom. Regressions between species richness and year indicate near significant negative trends for mid-depth ($P=0.06$) and overall ($P=0.08$), but insignificant relationships for shallow and deep depth strata (Fig. 7). With the exception of the deep depth stratum ($P=0.20$), significant positive relationships ($P<0.01$) were observed between species richness and the PDO. The number of fish species present within two depth strata (shallow and mid-depth) and overall increased during the warm PDO phase. Additionally, species richness indices declined within increasing depth strata (Fig. 7).

Based on minimum AIC values, the models which provided the best fit to changes in species richness during the survey period were either models incorporating only PDO indices (shallow, mid-depth, and overall) or models incorporating both year and PDO values (deep), but not models based solely on year (Table 2).

Discussion

The Pacific Coast groundfish fishery is exceedingly complex to manage because a wide range of species (90+), including a number of overfished and rebuilding stocks, are caught with the same trawl gear. Beginning in 2000, the PFMC initiated a series of measures designed to reduce catch along the west coast, including fleet reductions, closed areas, and catch restrictions. These measures were initiated in direct response to nine stocks being declared overfished from 1999 to 2002. Landed catch from 1980 through 2010 shows that groundfish harvests off Washington, Oregon, and California were significantly lower (rockfishes, flatfishes, sablefish) or relatively constant (Pacific hake, thornyheads) in recent years relative to historical rates (Fig. 8). This period of decreased catch corresponds to the implementation of the PFMC's management plan. And yet, despite much reduced fishing effort (and landings), overall survey indices of groundfish biomass off the western United States declined from 2003 through 2010. The PFMC's management directives also coincided with the period following expansion of the NWFSC's West Coast Goundfish Bottom Trawl Survey to annually include both the shelf region, as well as the upper continental slope waters along the entire coast (U.S.–Canada to U.S.–Mexico). We used data from this fishery-independent survey combined with information from 24 stock assessments since 2005 to attempt to unravel the causes for the decline in biomass indices despite strict adherence to fishery management plans.

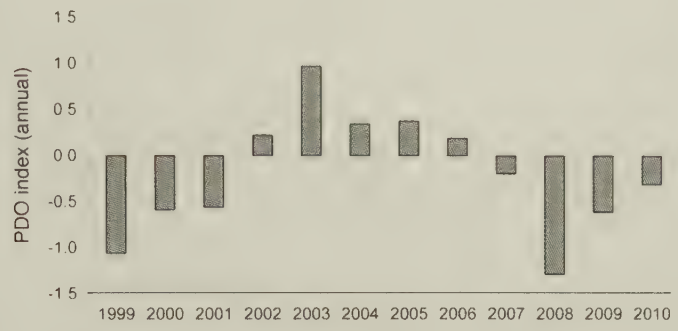

Figure 5

Annual variation in the Pacific Decadal Oscillation index (PDO) from January 1999 through December 2010 as it fluctuated between cool negative and warm positive phases. Annual values are the mean of the 12 months beginning in November of the year preceding the start of each annual survey and ending in October with the completion of the annual survey.

Our results indicated that from 2003 through 2010 individual groundfish stocks along the U.S. west coast responded in varying ways to the newly imposed management measures, with many of the overfished species of concern exhibiting increases in spawning stock biomass (PFMC, 2008a). However, despite improvements in individual stocks there has been a gradual decline in overall groundfish biomass, measured as the sum of the biomass indices for 60 abundant groundfish and two benthic invertebrate species, as well as in major groundfish groups (e.g., sharks, flatfishes, and rockfishes). Twenty of the 62 species described here significantly decreased in observed biomass from 2003 through 2010, whereas 6 species significantly increased. Of the remaining 36 species, 20 exhibited decreasing trends and 16 exhibited increasing trends. These changes indicate that the decline in biomass is not attributable to just a few species. Similar declines in Northwest Atlantic fish stocks have previously been attributed to a variety of factors including overfishing and environmental effects (Haedrich and Barnes, 1997). Hilborn et al. (in press) noted that the dramatic decline in catch can be interpreted in two ways: as an indication of collapsing stocks caused by overfishing, or as a demonstration that management has effectively reduced catch to prevent overfishing of sensitive species. However, the continued decline in overall observed biomass along the west coast suggests that reduced catch in itself may not be sufficient to prevent biomass from further decreasing when environmental conditions are poor. Hsieh et al. (2008) further concluded that fishing pressure reduces the resilience of exploited populations facing negative climatic effects.

By chance our study occurred during a period after the emergence of a particularly strong 1999 year class for many groundfish species inhabiting the California Current system (Haltuch and Hicks, 2009) and a period of changing environmental conditions as indicated by variability in the annual PDO index. The observed declining survey trends are consistent with natural and fishing-induced mortality estimated for the 1999 cohort in many stock assessments, especially flatfishes, sablefish, and Pacific hake (Schirripa, 2007; Haltuch and Hicks, 2009; Stewart et al., 2011). However, the prevalence of this large year class among many west coast groundfish and its gradual depletion over the survey period (2003–10) may not be entirely responsible for the dramatic decline in overall biomass estimated with data from our west coast fishery-independent survey.

The decline in biomass may additionally be tied to environmental conditions. The annual PDO index, a measure of climate variability, declined from a high value at the start of our standardized survey (2003) to low and negative values near the end of the series examined (2007–10). Numerous studies correlate shifts in the abundance and distribution of marine fish to oscillations in ocean conditions (Francis et al., 1998; Beamish et al., 1999; Hare et al., 1999). Within the northern California Current system, changes in salmon production (Mantua et al., 1997), landed sardine catch (Smith and Moser, 2003; Norton et al., 2008), and Pacific hake distribution (Benson et al., 2002) are linked to decadal-scale fluctuations in climate. Hollowed et al. (2001) further reported that production of commercial fish stocks (32 pelagic fish and groundfish species) in

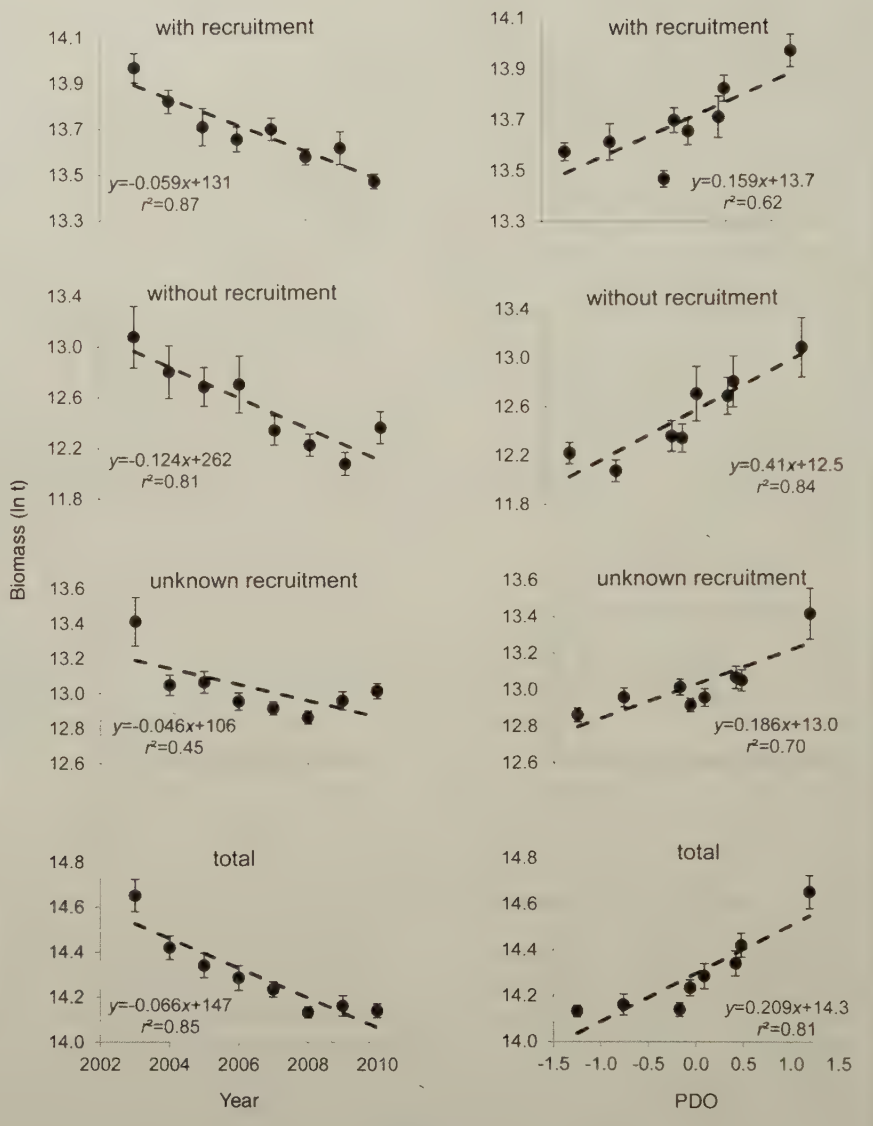

Figure 6

Expanded coast-wide biomass indices (natural log of biomass, [t]) and standard errors as a function of year and annual Pacific Decadal Oscillation (PDO) values for 62 dominant demersal taxa collected during the 2003–10 groundfish survey subdivided into three subgroups (with, without, and unknown recruitment) and summed overall (total). Regression equations for subgroups with significant ($P<0.05$) or near significant ($P<0.10$) trends are displayed in the figure. Significance levels (P) are listed in Table 2.

the North Pacific responded to climatic shifts. Major changes in coastal ocean productivity of the eastern Pacific are correlated with phase changes in the PDO and cold eras are associated with enhanced productivity. Warm periods are correlated with low productivity in the California current system (Brodeur and Ware, 1992; Hare and Francis, 1995) and the observed decrease in coastwide biomass could reflect the decline in biomass during the most recent warm period (2003–06) as productivity levels drop.

Results indicate that not only for individual species but also for species grouped taxonomically or by depth the change in biomass over time (2003–10) was variable. For the slope rockfish group (aurora rockfish [*Sebastes aurora*], bank rockfish [*Sebastes rufus*], blackgill rockfish, darkblotched rockfish, Pacific ocean perch, redbanded rockfish, [*Sebastes babcocki*], rougheye rockfish [*Sebastes aleutianus*], and splitnose rockfish) and the deepwater species group (mean depth >650 m) composed of brown cat shark (*Apristurus brunneus*),

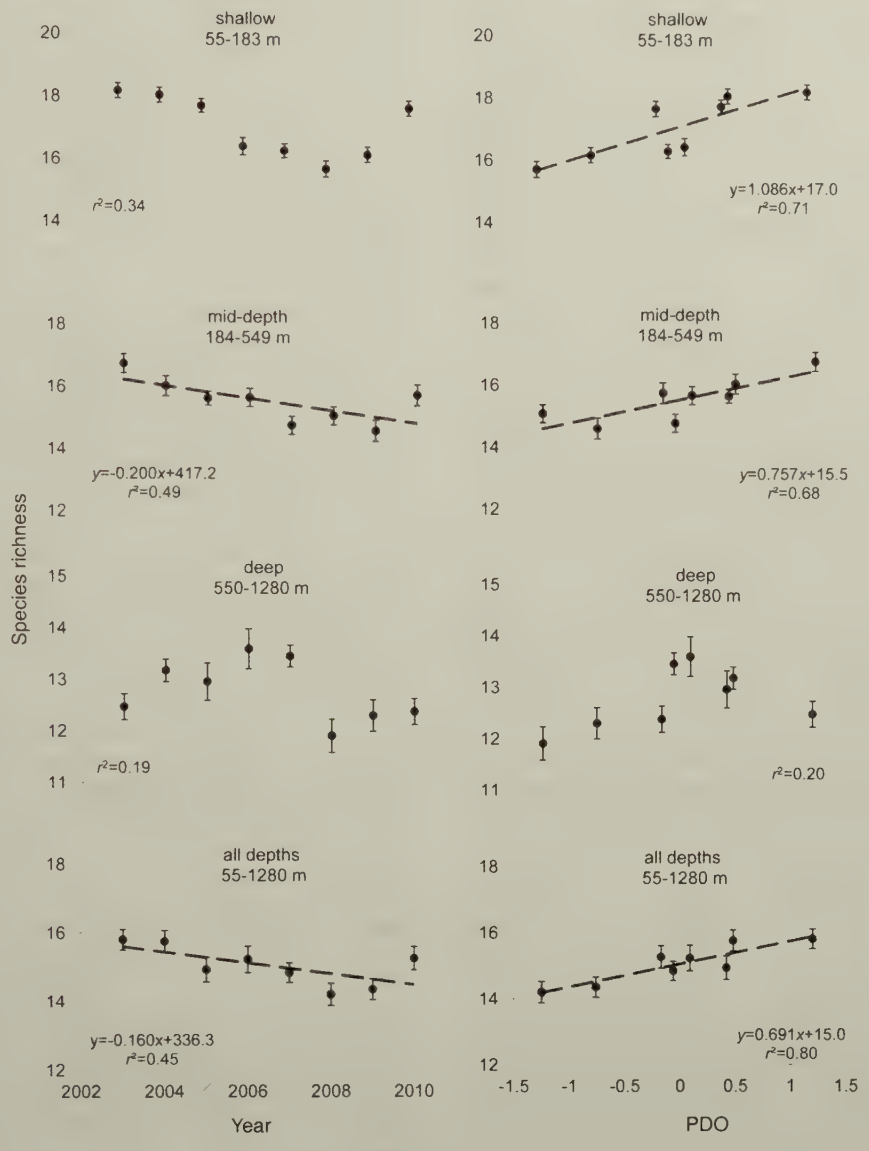

Figure 7

Coast-wide estimates of species richness (± standard error) by depth (shallow 55–183 m; mid 184–549 m; deep 550–1280 m; all depths combined 55–1280 m) versus year and annual Pacific Decadal Oscillation (PDO) values, 2003–10. Regression equations for relationships with significant (P<0.05) trends are displayed. Coefficients of determination (r^2) are shown here for the regression equations while significance levels (P) are shown in Table 2.

California slickhead (*Alepocephalus tenebrosus*), deepsea sole (*Embassichthys bathybius*), giant grenadier (*Albatrossia pectoralis*), Pacific flatnose (*Antimora microlepis*), Pacific grenadier (*Coryphaenoides acrolepis*), roughtail skate (*Bathyraja trachura*), snakehead eelpout (*Lycenchelys crotalinus*), twoline eelpout (*Bothrocara brunneum*), and grooved Tanner crab (*Chionoecetes tanneri*), no significant relationship with time was detected over the survey period. Thornyheads were the sole group to exhibit an overall positive correlation with time (with higher biomass occurring in recent years). Shallow to mid-water species (mean depth <500 m) consisting of groups composed of cartilaginous fish, flatfish, shelf rockfish, or a mixed subgroup of fish, and overall biomass all significantly declined over time. These declines occurred despite the classification of the west coast fishery as having the lowest overall exploitation rates of ten ecosystems examined by Worm et al. (2009) and multiple management measures introduced to reduce catch.

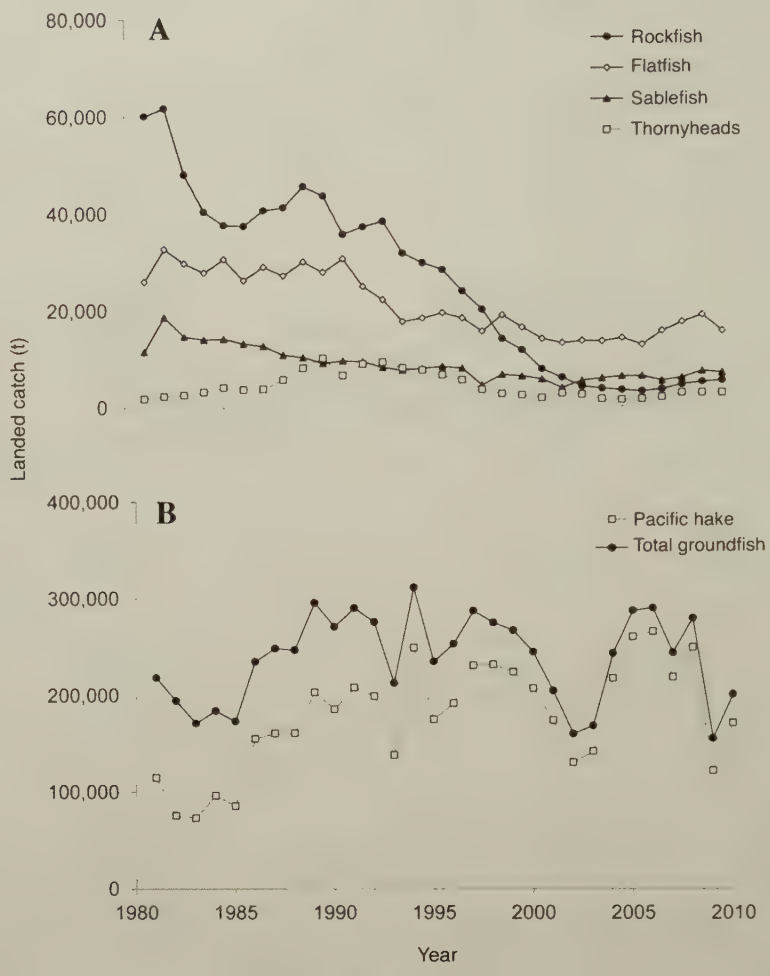

Figure 8

Landed catch (in metric tons, t) for (A) rockfish (*Sebastes* spp.), flatfish, sablefish (*Anoplopoma fimbria*), and thornyheads (*Sebastolobus* spp.), and (B) total groundfish and Pacific hake (*Merluccius productus*), off Washington, Oregon, and California from 1980 through 2010. Data were obtained from the Pacific Fisheries Information Network: http://pacfin.psmfc.org/pacfin_pub/data.php (accessed September 2011). Note the different scales for overall catch and Pacific hake (0–400,000 t) and for the remainder of the species (0–80,000 t).

To evaluate the decline in overall groundfish biomass indices off the western United States, despite much reduced fishing effort, we investigated two potential and perhaps overlapping factors: depletion after strong recruitment and environmental effects. Decreases in total biomass indices occur within an ecosystem when catch is greater than net population growth. To evaluate the contribution of these factors to the observed decline in biomass, we separated the species examined here into subgroups based on the presence or absence of strong recruitment during the late 1990s. We used information contained in 24 stock assessments to assign species to subgroups with strong recruitment (primarily in 1999), without strong recruitment, and with unknown recruitment. We developed regressions models for each subgroup and overall versus year, annual PDO indices, and including both variables. We assumed that year was a good proxy for depletion of exceptionally strong cohorts as they recruited to the groundfish fishery in subsequent years (Haltuch and Hicks, 2009). For multiple species with highly successful recruitment events in 1999, there has been a gradual decline in biomass since 2003. Regression models for total biomass of these species were best fitted by time, whereas regression models for those species without strong recruitment were best fitted to variation in climate as measured by annual PDO indices. Our analysis also indicated that for models comparing summed biomass for groups with

unknown recruitment and overall, the best fit incorporated both year and PDO indices combined. We think it is important to note that for all subgroups, particularly the group without species with known strong recruitment events, there is still a significant decrease in biomass indices over time. This decrease indicates that the depletion of an exceptionally strong 1999 year class for multiple species is not the only factor contributing to decreasing biomass of west coast demersal fish species. Despite the overall decline in biomass observed in recent years, very few of the species examined here are considered overfished (NMFS, 2009) and therefore a loss of yield cannot be inferred. However, the continued decline in overall observed biomass from 2003 to 2010, despite enactment of multiple management measures and reduced catch, emphasizes the need for the state of the ecosystem to be considered when setting catch limits. During periods of low ocean productivity, a precautionary approach is advised.

During the NWFSC bottom trawl survey, random, rare, and very large tows of schooling rockfish are occasionally taken. If a tow occurs near rocky but still trawlable habitat when schooling rockfishes are present, then very large catches of rockfish are possible (Stewart, 2007). Occurrence of these large catches may prevent detection of underlying biomass trends when only a small number of years are available for analysis, as with the 2003–10 survey. Although this phenomenon appears clear for canary and widow rockfish, for species like sharpchin and redbanded rockfish, it is harder to clearly separate large rare tows from an increase or decrease in biomass, and certainly random large catches and biomass trends may be occurring at the same time (Fig. 3).

The higher productivity associated with the cool PDO phase in the California Current system may have resulted in another strong recruitment event in 2008 (Ralston[3]) and if cool conditions continue, the associated higher productivity could promote enhanced growth and survival of groundfish. Our data indicate that the return to cool conditions in 2007–10 was followed by a slight increase in overall biomass in 2010—an increase that suggests a time lag between cool conditions and increased demersal biomass within the California Current. Although many rockfish species are long lived and exhibit highly variable recruitment, previous studies have additionally indicated that both rockfish recruitment and juvenile growth respond to broad indicators of productivity, and that juvenile abundance is correlated with large-scale oceanographic events such as El Niño–Southern Oscillation and the PDO (Ainley et al., 1993; Laidig et al., 2007). For now we find our results interesting and recognize that the value of the groundfish survey increases with each annual increment and over time will provide additional information to unravel these relationships.

[3] Ralston, S. 2011. Personal commun. National Marine Fisheries Service, Southwest Fisheries Science Center, Fisheries Ecology Division. Santa Cruz, CA 95060.

The best models to describe the variation in species richness (restricted to fish only) included the PDO indices (shallow, mid-depth, and overall) or a combination of the PDO indices and year (deep depths) but were not based on year alone. Species richness was positively correlated with the annual PDO index indicating that more species were present within the survey area and, in particular, at shallow and mid-depth strata during the warm phase of the PDO. Tolimieri and Levin (2006) and Tolimieri (2007) examined patterns of diversity in groundfish assemblages in relation to depth (200–1200 m) and latitude (33–37° N) along the U.S. Pacific Coast. They found, as we did, that species richness declined with depth (Fig. 7), but they did not examine changes over time or in relation to climate indices. However, their observation that patterns of diversity were correlated with temperature may partially support our observation of elevated species richness during the warm phase of the PDO. Tolimieri (2007) points out that latitude and depth are factors well known to correlate with diversity and assemblage structure. Both species richness and biomass decreased along the U.S. west coast for demersal groundfish as the PDO index shifted from a warm to a cool phase. Given that the swept area per haul remains constant, fewer species per haul are expected if the underlying population densities decrease; however, as demonstrated above, the densities for the 62 most abundant species exhibited variable trends from 2003 through 2010.

Mueter and Litzow (2008) provided convincing evidence of climate-linked changes in the distribution of demersal fishes in the Bering Sea (1982–2006), coupled with reorganization in community composition by latitude. They observed increases in both biomass and species richness in an area characterized by warming temperatures. Community-wide patterns indicated that taxa shifted northward and also were captured with increasing frequency at shallower stations from 1982 to 2006. Interestingly, they noted that mean species richness significantly increased within the portion of the survey area termed the "cold-pool" as it warmed over time, in a similar relationship to that observed here. Species richness along the U.S. west coast was elevated during the warmer phase of the PDO and lower during the cool phase. Changes in species richness are most likely caused by movement of species in response to environmental conditions (Trenkel and Cotter, 2009).

Understanding the mechanisms underlying the observed relationships between biomass indices, species diversity, depletion, and climate remains a challenge. However, Brodeur et al. (2008) recently related variations in the abundance of dominant ichthyoplankton in the northern California Current to oceanic and climatic indices, thus providing a link between climate and recruitment success. Both larval concentrations and diversity varied on a semidecadal basis in conjunction with fluctuations in the PDO. Zheng and Kruse (2006) found some evidence that recruitment variation in eastern Bering Sea crabs may be related to climate forcing, although interaction with groundfish predators likely

contributed to recruitment success as well. Brodeur and Ware (1992) and Sugimoto and Tadokoro (1997) both demonstrated changes in zooplankton biomass and distribution coupled with changes in ocean conditions, and Lenarz et al. (1995) reported reduced primary productivity and zooplankton biomass, coupled with poor rockfish recruitment off the west coast during El Niño events. Recruitment success of salmon within the northern California Current system has previously been tied to fluctuations in the PDO index (Mantua et al., 1997). Hollowed et al. (2001) examined the timing of the PDO and ENSO and correlated changes in both with recruitment success in groups such as flatfish and gadoids, but further study is needed to confirm their findings. Like others, they caution that additional factors could also affect biomass, species richness, and distributional changes such as density-dependent habitat selection, timing of migrations, changes in local currents, catchability, and shifts between nursery and feeding grounds (Swain et al., 1994; Delworth et al., 1997; Attrill and Power, 2002; Magill and Sayer, 2002). The interactions among climate variability, currents, and the seasonal strength of upwelling and downwelling is particularly interesting given our prior research where we directly linked changes in demersal biomass and species diversity to depressed oxygen levels along the Oregon shelf (Keller et al., 2010).

At the species level, changes appear driven by climate-induced variation in primary and secondary productivity and recruitment (Beaugrand et al., 2003; Steingrund and Gaard, 2005), although the nature of the relationship has not been deciphered. We recognize that the relatively short time series examined may increase the likelihood that the results are spurious. The observed tight correlations between total and grouped groundfish biomass indices and the PDO are expected if the underlying relationship results from reduced population growth due to poor environmental conditions or if environmental conditions, such as phase shifts in regional climate (Mantua et al., 1997; Hollowed et al., 2001; Castonguay et al., 2008) are also coupled with periodic strong recruitment events, such as the emergence of the 1999 year class.

Natural mortality for species with relatively high natural mortality rates could play an additional role in declining biomass indices. However, for rockfish with low natural mortality rates, it is likely that growth would be more important than mortality during most of the time period. The relationship between the PDO and biomass indices may also be due to changes in catchability or selectivity, rather than to actual population changes. A decrease could be due to higher selection of younger fish (i.e., to peak selection around age 4 or 5 and a decline afterwards). Although understanding the mechanisms supporting the relationships observed here remains problematic, our results demonstrate the importance of incorporating environmental conditions in management decisions. Despite enactment of highly effective management measures and the occurrence of periodic strong recruitment, biomass indices declined as oceanographic conditions changed throughout much of the survey period.

Acknowledgments

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A note on the von Bertalanffy growth function concerning the allocation of surplus energy to reproduction

Shuhei Ohnishi (contact author)[1]

Takashi Yamakawa[2]

Hiroshi Okamura[3]

Tatsuro Akamine[4]

Email address for contact author: ohnishi@scc.u-tokai.ac.jp

[1] School of Marine Science and Technology
Tokai University
Shimizu, Shizuoka 424-8610, Japan

[2] Graduate School of Agricultural and Life Sciences
The University of Tokyo
Bunkyo, Tokyo 113-8657, Japan

[3] National Research Institute of Far Seas Fisheries
Fisheries Research Agency
Yokohama, Kanagawa 236-8648, Japan

[4] National Research Institute of Fisheries Science
Fisheries Research Agency
Yokohama, Kanagawa 236-8648, Japan

Abstract—We propose an extended form of the von Bertalanffy growth function (VBGF), where the allocation of surplus energy to reproduction is considered. Any function can be used in our model to describe the ratio of energy allocation for reproduction to that for somatic growth. As an example, two models for energy allocation were derived: a step-function and a logistic function. The extended model can jointly describe growth in adult and juvenile stages. The change in growth rate between the two stages can be either gradual or steep; the latter gives a biphasic VBGF. The results of curve fitting indicated that a consideration of reproductive energy is meaningful for model extension. By controlling parameter values, our comprehensive model gives various growth curve shapes ranging from indeterminate to determinate growth. An increase in the number of parameters is unavoidable in practical applications of this new model. Additional information on reproduction will improve the reliability of model estimates.

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The von Bertalanffy growth function (VBGF) has been used to analyze somatic growth data in a wide range of studies. It is now commonly put into practice to partially reparameterize the VBGF parameters to avoid their covariation and to ensure statistical accuracy (Quinn and Deriso, 1999).

Although variations in the growth rate influenced by extrinsic environmental fluctuations have been examined in many studies, we propose that intrinsic physiological dynamics are also of great importance. The interaction between growth rate and sexual maturation has often been debated in life history studies (Roff, 1984; Beverton, 1992; Jensen, 1996). Mathematical treatments for representing the switch in energy allocation between growth and reproduction have been introduced to discuss optimal life-history strategies (Roff, 1983; Kozłowski, 1992, 1996; Kozłowski and Teriokhin, 1999). When the energy budget of fishes has been quantified, dynamics of the energy distribution between growth and reproduction have often been considered in simulated scenarios (Jørgensen and Fiksen, 2006; Pecquerie et al., 2009).

The effects of reproductive energy should also be important for practical curve fitting studies. A biphasic growth model derived by connecting two independent VBGFs at an arbitrary age is often employed for curve fitting (Soriano et al., 1992; Porch et al., 2002; Araya and Cubillos, 2006; Quince et al., 2008a, 2008b; Alós et al., 2010; Tribuzio et al., 2010). Although a biphasic VBGF is one approach used to account for inflections in growth and is similar to the higher-parameter model (Schnute and Richards, 1990), results of model selection based on the Akaike information criterion (AIC; Akaike, 1973) often indicate that the biphasic VBGF is a more suitable model than the original monophasic VBGF (Porch et al., 2002; Araya and Cubillos, 2006; Tribuzio et al., 2010). The better fit implies that the delay in growth due to a reallocation of energy may be detected as a change in the growth trajectory.

Day and Taylor (1997) and Czarnołęski and Kozłowski (1998) identified the lack of an explicit formula for the reproductive process in the VBGF. Although the biphasic VBGF is an empirical approach, a deductive model that can incorporate both growth and reproduction should be developed to help to understand the process of energy allocation and to improve curve fit. In this study, we begin with an extension of the VBGF with respect to a continuous change in energy allocation. We also present an application of curve fitting and model selection. An overview of changes in growth-curve shapes is subsequently shown. Finally, we briefly discuss the features of our model.

Methods

We start with the general form of VBGF given by

$$\frac{dw}{dt} = hw^{2/3} - kw, \tag{1}$$

where w, t, h, and k are body weight, age, and coefficients of anabolism and catabolism, respectively. The right hand side of Equation 1 is the total production rate of surplus energy.

If we consider the reallocation of surplus energy for reproduction, Equation 1 can be expanded as

$$\frac{dw}{dt} + c\frac{df}{dt} = hw^{2/3} - kw. \tag{2}$$

Two newly introduced terms, f and c, denote the cumulative energy investment for reproduction until age t and the conversion factor of reproductive energy to body weight, respectively. Note that f is not equivalent to the weight of the gamete (i.e., eggs or spermatozoa). Equation 2 is equivalent to the exoskeleton growth model (Ohnishi and Akamine, 2006) in that energy allocation to activities or appendages unrelated to somatic growth are explicitly described.

Suppose $w=\beta l^3$, where l is body length and β is a constant proportionality coefficient. Dividing $dw/dt=3\beta l^2 dl/dt$ by each side of Equation 2 and substituting $w=\beta l^3$ yields the following equation:

$$\frac{dl}{dt} = \left(\frac{dw}{dt}\right)\left(\frac{dw}{dt} + c\frac{df}{dt}\right)^{-1} K\left(l_\infty - l\right), \tag{3}$$

where $K=k/3$ and $l_\infty (=hk^{-1}\beta^{-1/3})$ is the asymptotic length. Let p be the ratio ($0\le p\le 1$) of energy invested to reproduction against total surplus energy such that

$$p = \left(c\frac{df}{dt}\right)\left(\frac{dw}{dt} + c\frac{df}{dt}\right)^{-1}. \tag{4}$$

Hence, Equation 3 becomes

$$\frac{dl}{dt} = (1-p)K\left(l_\infty - l\right). \tag{5}$$

Equation 5 comprehensively describes two types of life history strategies, which can be generally classified as determinate and indeterminate growth (Lincoln et al., 1998). It tends towards determinate growth when p is close to 1.0 and otherwise towards indeterminate growth. The value of the parameter p increases with sexual maturation, and it can be replaced by $p(w)$, $p(l)$, or $p(t)$ as a function of size or age. In particular, a mathematical treatment is easy when $p\equiv p(t)$. Given that $l=0$ at $t=t_0$ (the initial condition), the general form of the growth function is given as

$$l = l_\infty\left(1 - e^{-KT(t)}\right), \text{ where } T(t) = \int_{t_0}^{t}\left\{1 - p(s)\right\} ds. \tag{6}$$

It should be noted that $p(t)$ can take an arbitrary functional form with $0\le p(t)\le 1$.

Among the various possible forms of $p(t)$, we propose the following two models that are relatively easy to derive. The first is a model where $p(t)$ exhibits a discontinuous change in age at maturity t_m, such that $p(t)=0$ ($t<t_m$) and $p(t)=v$ ($t\ge t_m$), where $0\le v\le 1$. In this case, $T(t)$ is defined by

$$T(t) = \begin{cases} t - t_0 & (t < t_m) \\ t - t_0 - v\left(t - t_m\right) & \left(t \ge t_m\right) \end{cases}. \tag{7}$$

Equation 7 represents the time delay to attain a certain body size in $t\ge t_m$ due to change in energy allocation. Consequently, the growth curve becomes biphasic, combining two independent VBGFs.

The alternative model assumes that $p(t)$ changes continuously throughout an individual's lifetime. In particular, an S-type curve that has an inflection point around $t=t_m$ is suitable for describing a change in $p(t)$ due to sexual maturation. Let $p(t)$ be $p(t)=v/(1+\exp(-a(t-t_m)))$ as a general logistic curve such that the analytical solution for $T(t)$ is given by

$$T(t) = (1-v)\left(t - t_0\right) - \frac{v}{a}\left\{\log\left(1 + e^{-a(t-t_m)}\right) - \log\left(1 + e^{-a(t_0-t_m)}\right)\right\}, \tag{8}$$

where v and a are the upper limit of the allocation rate in reproductive energy and the rapidity of maturation, respectively. The logistic function converges to a step-function when $a\to\infty$. By inspection, Equation 7 is a special case of Equation 8.

The solution for Equation 5 is complicated when $p\equiv p(l)$ (or $p\equiv p(w)$) such that

$$\int_0^l \frac{1}{\left(l_\infty - x\right)\left(1 - p(x)\right)} dx - K\left(t - t_0\right) = 0. \quad [0 \le p < 1] \tag{9}$$

The explicit solution for l is a biphasic VBGF when $p(l)$ is a step-function that has discontinuous switching at

Table 1

Parameter estimates for two types of von Bertalanffy growth functions (VBGFs). Both types of VBGF have three common parameters: asymptotic length (l_∞), growth coefficient (K), and initial condition of age (t_0). Additional parameters, namely age at maturity (t_m), the upper limit of the allocation rate in reproductive energy (v), and rapidity of maturation (a), were used in the extended model. Values within parentheses show the square root of the variance of the estimates derived from the matrix inverse of the Hessian matrix. The ΔAIC shows the relative difference of the Akaike information criterion (AIC) value compared with the minimum AIC.

Type of VBGF	l_∞	K	t_0	t_m	v	a	AIC	ΔAIC
Conventional model	260.72	0.34	−0.45	—	—	—	26881.3	20.8
	(1.51)	(0.01)	(0.04)					
Extended model	463.01	0.15	−0.77	3.41	0.79	1.01	26860.5	0
	(49.08)	(0.01)	(0.14)	(0.35)	(0.05)	(0.21)		

the boundary of mature "size." In most cases, however, it is not easy to obtain an explicit solution, as shown in Equation 6, owing to the complexity of the integrand in Equation 9.

Allocated reproductive energy can be derived as follows by rearranging Equation 4 with the condition $p \equiv p(t)$ as

$$\left(1-p(t)\right)c\frac{df}{dt}=p(t)\frac{dw}{dt}.$$

Substituting $dw/dt=3\beta l^2 dl/dt$ and Equation 5 into this equation, one obtains

$$\frac{df}{dt}=\frac{3\beta K}{c}p(t)l^2\left(l_\infty-l\right), \quad (10)$$

$$f=\frac{3\beta K}{c}\int_{t_0}^{t}p(s)l^2\left(l_\infty-l\right)ds. \quad (11)$$

Equation 10 represents the instantaneous reproductive energy at age t. Equation 11 shows the cumulative investment of reproductive energy until age t. Thus, changes in two quantities (body size in Eq. 6 and energy investment in Eq. 10) are treated in an extended VBGF.

We fitted the growth curve in Equations 6 and 8 to individual measurements in length-at-age as $L_i (i=1,\ldots, N)$, where N is the total number of samples. Parameters were estimated by minimizing the residual sum of squares of $S=\sum_i (L_i-l_i)^2$. The numerical optimization for S was accomplished by using the quasi-Newton method (BFGS algorithm) in "optim( )" with R statistical software (R Development Core Team, 2011). The comparison between this model and the original monophasic VBGF was based on the AIC value as follows: $AIC=N\log S+2\theta$, where θ is the number of free parameters.

We used measurement data on willowy flounder (*Tanakius kitaharai*) males collected by bottom-trawl surveys in the coastal area of Fukushima Prefecture, Japan, from 2004 to 2006. The sample size was n=2169. Age ranged from 1.38 to 14.30 years and length ranged from 113 to 298 mm (standard length). Otoliths were used to determine yearly ages and dates of birth were assigned as January 1st.

Results

Results for curve fitting and model selection are summarized in Table 1 and Figure 1. As shown in Table 1, the AIC difference (ΔAIC=20.8) between the two types of VBGF suggests that the trajectory given by the extended model more appropriately described lifetime growth. This result implies that a consideration of reproductive energy can be meaningful for model extensions. The variance of two common parameters (i.e., l_∞ and t_0) in the extended model was larger than that in the conventional VBGF (Table 1).

Twelve types of energy allocation schedules, $p(t)$, and the corresponding somatic growth (in length l) based on different combinations of parameter values in Equation 8 (v=0.4, 0.6, 0.8, 1.0 and a=1, 3, 100) are shown in Figure 2. The behavior of df/dt and f describing the energy investment in reproduction is shown in Figure 3.

When v=0, the growth curve is identical to the original VBGF (Fig. 2). Although somatic growth curves generated by lower v values (i.e., v=0.4, Fig. 2, A–C) do not differ substantially from the original VBGF, there are distinctive differences for shapes with higher v values (i.e., v=0.8, 1.0, Fig. 2, G–L). In these cases, the somatic growth of the adult and juvenile stages can be clearly distinguished. Gradual but steady growth after maturation is typical with indeterminate growth (Fig. 2, A–I). We can see a continuous phase shift of indeterminate growth in Figure 2. When v=1.0, the growth rate after maturation converges to zero because most surplus energy is devoted to reproduction, generating more determinate growth (Fig. 2, J–L).

The variation in a leads to a difference in the degree of continuity of growth rate during the sexual maturation transition period (Fig. 2, A, D, G, and J vs. Fig. 2, C, F, I, and L). The curves given by sufficiently high a (a=100) represent biphasic VBGF resulting from an abrupt change in growth rate around age t_m (Fig. 2, C, F, I, and L).

In Figure 3, an apex can be found on the convex shape of df/dt, and the height and degree of curvature changes according to the values of v and a. An increase in the value of v raises the reproductive investment $df/$

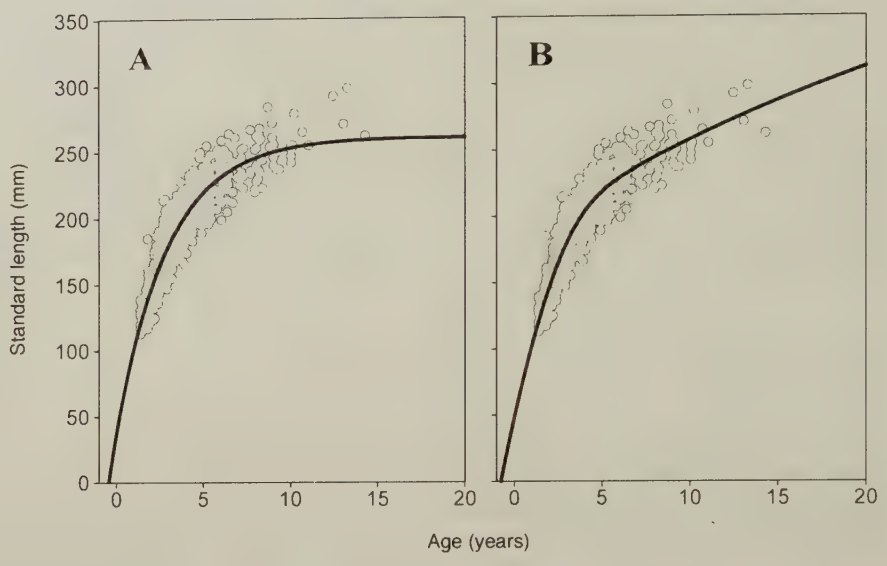

Figure 1

Two types of growth curve estimated with the conventional von Bertalanffy growth function (**A**) and with the extended von Bertalanffy growth function (**B**) for individual measurement data of the willowy flounder (*Tanakius kitaharai*) male (n=2169).

dt and shifts the maximum df/dt to older ages. When v=1.0 (Fig. 3, J–L), df/dt converges to a constant value after maturation as a result of determinate growth and constant surplus energy, defined by Equation 2. Lower a values show a slower initial rise in df/dt around t_m (Fig. 3, A, D, G, and J), whereas higher a values yield a steeper initial rise in df/dt around t_m (Fig. 3, C, F, I, and L).

Discussion

A notable feature of our model is that energy allocation can be quantified by the arbitrary functional form $p(\cdot)$. The introduction of $p(\cdot)$ provides a unified platform to treat the trade-off between somatic growth and reproduction. The extended model can jointly describe adult and juvenile growth. The change in growth rate between the two stages can be either gradual or steep, with the latter case showing a biphasic VBGF. By controlling the value of $p(\cdot)$, our comprehensive model yields various shapes of growth curves that range from indeterminate to determinate growth. Therefore, our model can be used for life history studies, as well as practical curve fitting studies. When allocation dynamics are not fully described by a simple model, such as seen in Equation 8, additional parameters beyond a, v, and t_m, or a particularly designed form of $p(\cdot)$ would be useful for further model development.

The extended VBGF in Equation 5 can theoretically incorporate an unlimited number of parameters. However, an increase in the number of free parameters in $p(\cdot)$ will be disadvantageous for model estimation because the functional form of $p(\cdot)$ does not directly appear in the age-length relationship. Increases in the variance of estimates imply instability due to curve fitting (Table 1). Therefore, it is necessary to consider methods of overcoming the trade-off between an increased number of parameters and estimation stability. Data sets other than those for length-at-age data will be useful for estimating the parameters in $p(\cdot)$ because the dynamics of $p(\cdot)$ are readily apparent in the behavior of df/dt (Fig. 3) rather than in length (Fig. 2). We expect that the robustness of this estimation will be improved by means of a combined likelihood-function (Martin and Cook, 1990; Eveson et al., 2004) described by two heterogeneous relationships: length-at-age and reproductive energy-at-age.

Our model development has similarities to that of Lester et al. (2004). Both studies explicitly give a growth function that can quantify a delay in somatic growth due to reproductive energy allocation. Lester et al. (2004) initially assumed a linear function of premature growth in length and derived the conventional VBGF by introducing an intensive energy investment at postmature ages. Additionally, Lester et al. (2004) assumed that the ratio of gonad to body weight at postmature ages is constant. This assumption causes the linear function to yield a delay in growth after maturation equivalent to that yielded with the VBGF. Alternatively, our model derivation started from the VBGF. Additional hypotheses for model formulation other than ours and those of Lester et al. (2004) are possible. Hence, the adequacy of these assumptions for model derivation must be evaluated with a wide range of practical applications.

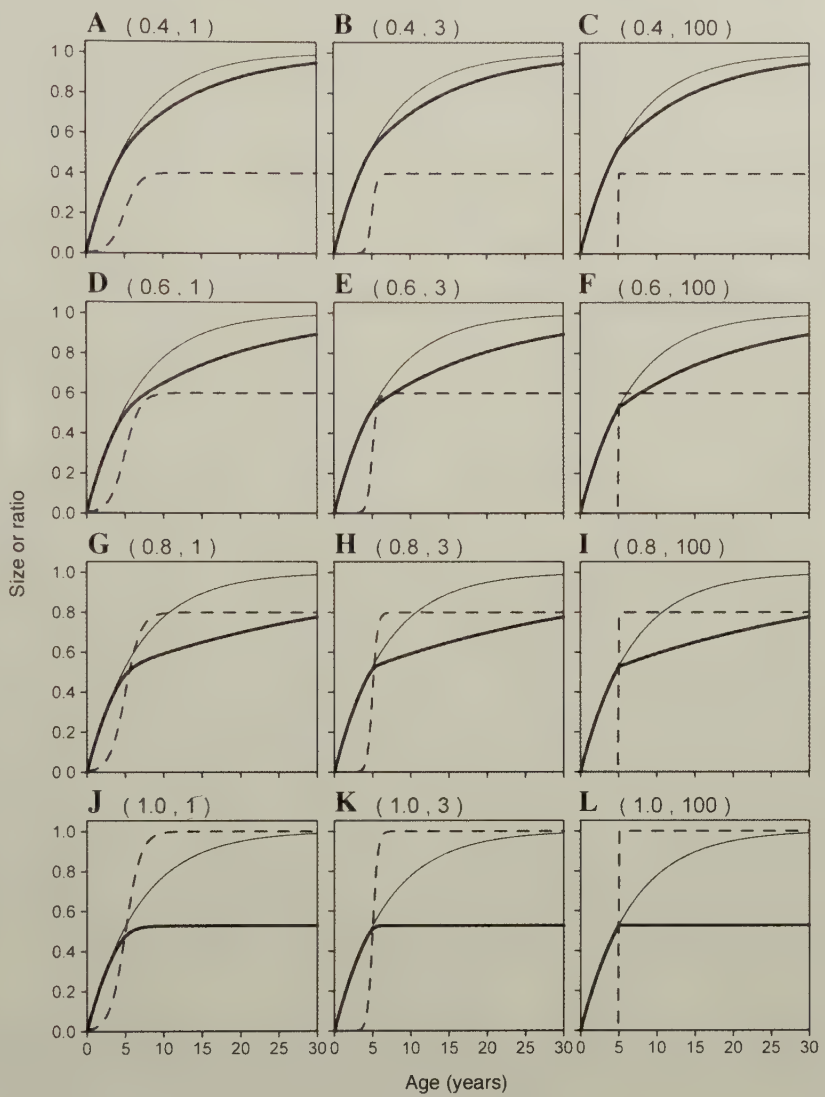

Figure 2

Variation in somatic growth due to differences in energy allocation (**A–L**). Thick, thin, and broken lines correspond to growth in length $l(t)$, growth in length $l(t)$ with $v=0$ (i.e., the original von Bertalanffy growth function), and the energy allocation function $p(t)$, respectively. The numerical values in parentheses correspond to the combination of parameters v(=0.4, 0.6, 0.8, 1.0) and α(=1, 3, 100) employed in $p(t)$. The parameters used for all cases include the following: β=1.0, c=1.0, K=0.15, l_∞=1.0, t_0=0, and t_m=5.

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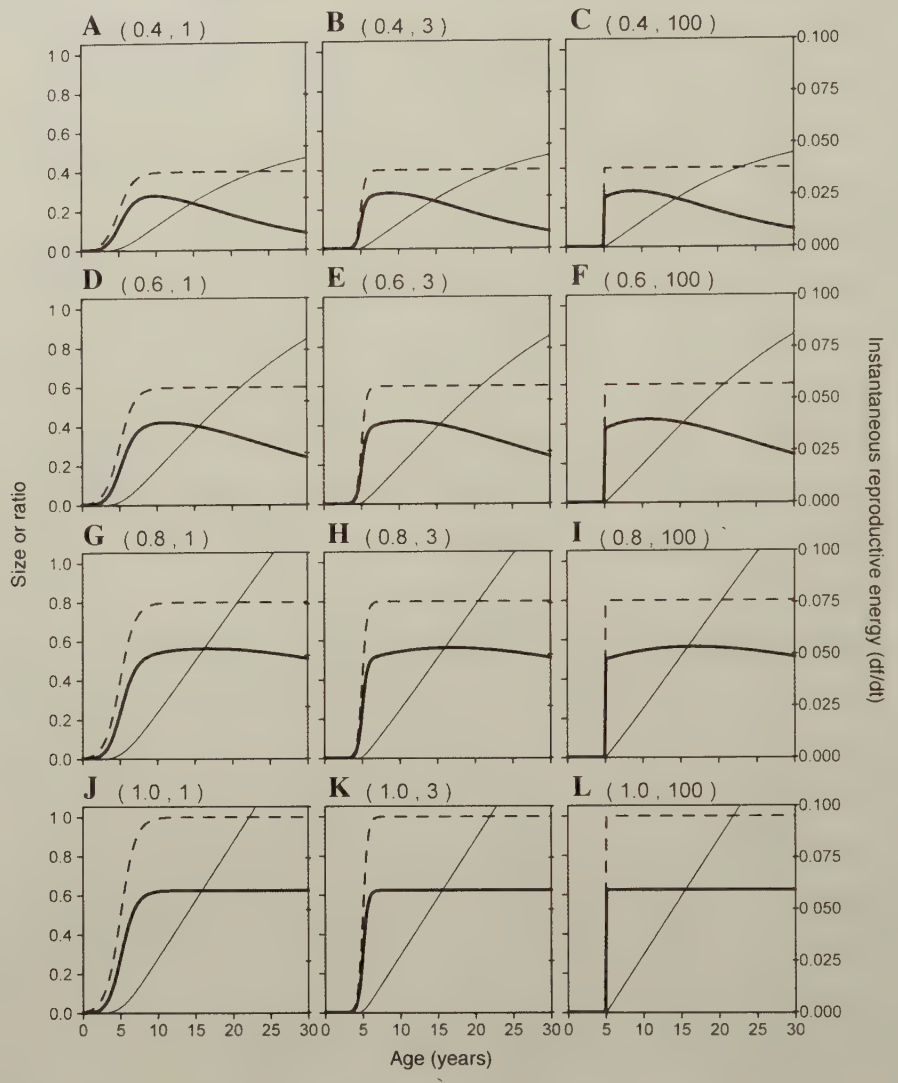

Figure 3

Variation in variables related to reproduction that result from differences in energy allocation (**A–L**). Thick, thin, and broken lines correspond to the instantaneous reproductive energy df/dt, cumulative energy investment $f(t)$, and the energy allocation function $p(t)$, respectively. The numerical values in parentheses correspond to the combination of parameters υ(=0.4, 0.6, 0.8, 1.0) and a(=1, 3, 100) employed in $p(t)$. The parameters used for all cases include the following: β=1.0, c=1.0, K=0.15, l_∞=1.0, t_0=0, and t_m=5.

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Gillnet selectivity for juvenile blacktip sharks (*Carcharhinus limbatus*)

Ivy E. Baremore (contact author)[1]
Dana M. Bethea[1]
Kate I. Andrews[2]

Email address for contact author: Ivy.Baremore@noaa.gov

[1] Panama City Laboratory
Southeast Fisheries Science Center
National Marine Fisheries Service
National Oceanic and Atmospheric Administration
3500 Delwood Beach Rd.
Panama City, Florida 32408

[2] Beaufort Laboratory
Southeast Fisheries Science Center
National Marine Fisheries Service
National Oceanic and Atmospheric Administration
101 Pivers Island Road
Beaufort, North Carolina 28516-9722

Abstract—Gillnet mesh selectivity parameters were estimated for juvenile blacktip sharks (*Carcharhinus limbatus*) by using length data from an experimental fishery-independent gillnet survey in the northeastern Gulf of Mexico. Length data for 1720 blacktip sharks were collected over 17 years (1994–2010) with seven mesh sizes ranging from 7.6 to 20.3 cm. Four selectivity models, a normal model assuming fixed spread, a normal model assuming that spread is proportional to mesh size, a log-normal model, and a gamma model were fitted to the data by using the SELECT (share each length's catch total) method. Each model was run twice under separate assumptions of 1) equal fishing intensity; and 2) fishing intensity proportional to mesh size. The normal, fixed-spread selectivity curve where fishing intensity is assumed to be proportional to mesh size provided the best fit to the data according to model deviance estimates and was chosen as the best model. Results indicate that juvenile blacktip sharks are susceptible as bycatch in some commercial gillnet fisheries.

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In the late 1980s, a gillnet fishery for sharks developed in the Atlantic Ocean off the coasts of Florida and Georgia (Trent et al., 1997). Fishing area varied with seasons, and shark drift gillnet vessels operated in nearshore waters between 4.8 and 14.4 km offshore, ranging from West Palm Beach, Florida (~26°46′N), to Altamaha Sound, Georgia (~31°45′N). A variety of methods were used to deploy gillnets, including drifting the net on the surface (Trent et al., 1997), striking around a school of sharks (Carlson and Baremore[1]), and anchoring the net to the bottom (Carlson and Bethea, 2007). Fishermen targeted a variety of coastal species of sharks, from blacktip sharks (*Carcharhinus limbatus*) to Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*) depending on market conditions and fishery closures. Over the last 10 years, the size and scope of the commercial shark gillnet fishery has decreased primarily owing to regulations that restrict gear, fishing areas, and trip limits for sharks. In 2008, Amendment 2 to the Consolidated Atlantic Highly Migratory Species Fishery Management Plan (NMFS, 2008) limited landings of large coastal sharks to 33 sharks per trip. The high cost of fuel and low market value for shark meat, in conjunction with these regulations, caused most commercial fishermen in the U.S. south Atlantic Ocean to abandon the gillnet fishery for sharks.

Although shark-targeted gillnet trips are currently rare in the U.S. Atlantic Ocean, blacktip sharks are still caught as bycatch in other gillnet fisheries that target species such as Spanish mackerel (*Scomberomorus maculatus*) and king mackerel (*S. cavalla*) (Passerotti et al., 2010; Thorpe and Frierson, 2009). These coastal teleost gillnet fisheries are expansive, and had more than 65 active fishing vessels in 2010.[2] The fishing locations of these vessels span the U.S. east coast throughout the range of the blacktip shark.

The blacktip shark is a cosmopolitan species, ranging from Massachu-

[1] Carlson, J. K., and I. E. Baremore. 2003. The directed shark gillnet fishery: catch and bycatch 2003, NOAA Sustainable Fisheries Division Contribution PCB-03/07, 8 p. Panama City Laboratory, National Marine Fisheries Service, Panama City, Florida. [Available from http://www.sefsc.noaa.gov/labs/panama/documents/observer_documents/gillnet/SDG2003.pdf, accessed December 2011.]

[2] Southeast Fisheries Science Center Coastal Fisheries Logbook, available at http://www.sefsc.noaa.gov/fisheries/reporting.htm, accessed March 2011.

setts throughout the Gulf of Mexico in U.S. coastal waters (McEachran and Fechhelm, 1998). Juvenile blacktip sharks use nursery areas such as bays and nearshore habitats during spring and summer months (Castro, 1993; Heupel and Hueter, 2002). Because of their range and life history characteristics, juvenile blacktip sharks are likely to encounter commercial gillnets.

Gillnet selection curves are a useful way to represent the retention probabilities of different mesh sizes for a given species of fish. Retention probability by gillnets is usually considered to be dome-shaped and can be described by the equation

$$r_j(l_i) = \exp\left(-\frac{(1-\mu_j)^2}{2\sigma_j^2}\right),$$

where $r_j(l_i)$ is the retention probability that a fish of length l in size class i is caught by mesh size j, and μ and σ represent the mean and spread of the curve (Millar and Fryer, 1999). However, the selection curve may be skewed because of snagging, rolling, or entangling of animals, and can result in a gamma or lognormal curve (Millar and Fryer, 1999).

Generally, selectivity can be measured in two ways: directly and indirectly (Millar and Fryer, 1999). Direct experiments are performed on a population for which the size distribution is known, and size selection is calculated by comparison of the population with the catch distributions. Indirect, or comparative, experiments are more common and usually involve simultaneously fishing gillnets of differing mesh sizes with equal effort.

Commercial fishing gear selectivity curves are incorporated into modern stock assessment models, and changes in the parameters have the potential to impact the assessed status of the stock (Maunder, 2002). Size selectivity is used in the estimation of the length-frequency of a stock, estimation of fishing-induced mortality, and in age-based assessment models (Millar and Fryer, 1999). Although important for the stock assessment models, fishery-independent selectivity models are rare for many large shark species (McAuley et al., 2007). Selectivity for bycatch species is also becoming an important issue in stock assessment, but direct estimates are likewise rare for most fisheries. The goal of this study is to determine the relationship between gillnet mesh size and selectivity for juvenile blacktip sharks using fishery-independent data.

Materials and methods

Sampling

Data necessary for indirect calculation of gillnet mesh selectivities were obtained from the Gulf of Mexico Shark Pupping and Nursery (GULFSPAN) survey, which is a fishery-independent gillnet survey of coastal shark populations in the northeastern Gulf of Mexico (Carlson and Brusher, 1999). Catch data for *C. limbatus* were collated over 17 years (1994–2010) from five bay systems in northwest Florida: St. Andrew Bay, Crooked Island Sound, St. Joseph Bay, the gulf side of St. Vincent Island, and Apalachicola Bay (Fig. 1).

Six gillnet panels of differing stretched mesh sizes were strung together in increasing mesh size, anchored, and fished concurrently as a single gillnet. Each panel was 30.1 m long and 3.4 m deep (Table 1). From 1994 through 2005, stretched mesh sizes ranged from 8.9 cm to 14.0 cm, increasing by 1.3-cm (0.5-in) intervals, with an additional panel of 20.3 cm. In 2006, the 20.3-cm panel was removed and a 7.6-cm panel was added *ad hoc*. The largest mesh panel was removed because of its historically low catch of juvenile small coastal shark species, and the 7.6-cm panel was added to increase catch of small neonatal sharks. Unless otherwise indicated, all mesh sizes reported in the present study are stretched mesh sizes.

Sampling occurred each year from late March through October. Net set locations within bay systems were randomly chosen over a variety of habitat and depth combinations. The majority of sets were short (<1 hr) as a means of reducing mortality, especially when water temperatures were above 25°C. However, some nets were soaked for longer periods of time, depending on the research priorities at the time. Captured sharks were removed from the net, their sex was determined, and they were measured for fork length (FL) on a rigid measuring board in a straight line from the tip of the nose to the fork in the tail. Sharks in poor condition were sacrificed for research projects and those in good condition were tagged and released. Maturity state was determined by clasper calcification for males, internal examination for sacrificed female sharks, and released females were considered to be mature when greater than 115 cm FL (Carlson et al., 2006). Sexes were combined for data analyses.

Data analysis

Catch data were pooled by mesh size into 5-cm-FL size bins, and the midpoint of each size class (l_i) was used to calculate a selectivity curve for each mesh size (Millar and Holst, 1997). Four gillnet selectivity models were fitted to the l_i for each mesh size (m_j) (Millar and Holst, 1997), by using the SELECT (share each length's catch total) method (Millar and Holst, 1997; Millar and Fryer, 1999; Millar, 2003, 2010). The selection curves were fitted to the data by using the "gillnetfunctions" package in R statistical software (Millar, 2003, 2010; R Development Core Team, 2009). The SELECT method applies the method of maximum likelihood, which estimates selectivity parameters from a general log-linear model. The expected catch of sharks of length class i in gillnet j is described by

$$v_{ij} = p_j \lambda_i r_j, \quad (1)$$

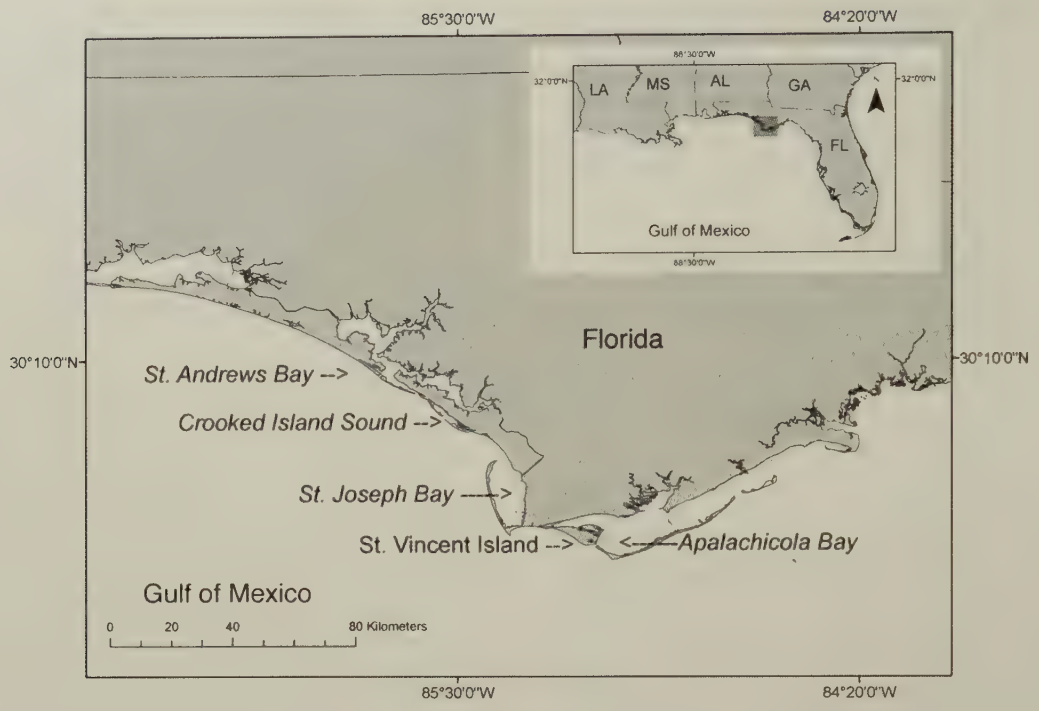

Figure 1

Location of the Gulf of Mexico Shark Pupping and Nursery (GULFSPAN) survey in northwest Florida. Sampling sites were located in St. Andrew Bay, Crooked Island Sound, St. Joseph Bay, the gulf side of St. Vincent Island, and Apalachicola Bay. Sampling occurred from 1994 through 2010.

Table 1

Gillnet specifications used in the Gulf of Mexico Shark Pupping and Nursery (GULFSPAN) survey 1994–2010. For all net configurations, the hanging ratio (length to height ratio of the meshes) was 0.5, leadline weight was 4.5 kg, 2.3 kg of buoyancy was used, and each panel length was 30.1 m.

Stretch mesh size (in/cm)	Twine size no.	No. of meshes deep	Thickness of twine (mm)	Breaking strength (kg)	Years fished
3.0/7.6	208	45	0.52	11.8	2006–2010
3.5/8.9	208	40	0.52	11.8	1994–2010
4.0/10.2	208	35	0.52	11.8	1994–2010
4.5/11.4	208	35	0.52	11.8	1994–2010
5.0/12.7	277	30	0.62	18.2	1994–2010
5.5/14.0	277	25	0.62	18.2	1994–2010
8.0/20.3	24	20	1.00	115.9	1994–2005

where p_j = the relative fishing intensity of gillnet j:
λ_i = the abundance of sharks in length class i; and
r_j = the selection curve for each gillnet j.

Relative fishing intensity represents fishing effort and fishing intensity combined and is the conditional probability that a fish contacted gillnet panel j, with the assumption that it made single contact with the entire combined gillnet panel (Millar, 1992). The normal, gamma, and lognormal models observe geometric similarity (mean μ_j and spread σ_j proportional to mesh size), whereas the normal model with fixed spread is not geometrically similar (mean μ_j and spread σ_j equal across mesh sizes). When p_j is assumed to be equal among mesh sizes, the form of the log-linear model is as follows:

$$\log(v_{ij}) = factor(l_i) + \beta_1 \cdot f_1(m_j, j) + \beta_2 \cdot f_2(m_j, j), \quad (2)$$

Table 2

Selectivity curves for normal, gamma, and lognormal models used to estimate gillnet selectivity for blacktip sharks (*Carcharhinus limbatus*): m_j is the mesh size for panel j (j=1–7 panels) and l_i is the midpoint of length class i (i=1–22 length classes). Relative fishing intensity is modeled separately. Equations in the right hand column are the last two terms in the log-linear model

$$\beta_1 = -\frac{a_1}{a_2}, \beta_2 = -\frac{1}{2a_2}, f_1(m_j, l_i) = \frac{l_i}{m_j}, f_2(m_j, l_i) = \frac{l_i^2}{m_j^2}.$$

Model	Selection curve	$\beta_1 \cdot f_1(m_j, l_i) + \beta_2 \cdot f_2(m_j, l_i)$
Normal: fixed spread	$\exp\left(-\frac{(l_i - k \cdot m_j)^2}{2\sigma^2}\right)$	$\left(\frac{k}{\sigma^2}\right) \cdot (l_i \cdot m_j) + \left(-\frac{k^2}{2\sigma^2}\right) \cdot m_j^2$
Normal: proportional spread	$\exp\left(-\frac{(l_i - a_1 \cdot m_j)^2}{2a_2 \cdot m_j^2}\right)$	$\left(\frac{a_1}{a_2}\right) \cdot \left(\frac{l_i}{m_j}\right) + \left(-\frac{1}{2a_2}\right) \cdot \left(\frac{l_i}{m_j}\right)^2$
Gamma: proportional spread	$\left(\frac{l_i}{(\alpha-1) \cdot k \cdot m_j}\right)^{\alpha-1} \exp\left(\alpha - 1 - \frac{l_i}{k \cdot m_j}\right)$	$[\alpha - 1] \cdot \left(\log\left(\frac{l_i}{m_j}\right)\right) + \left(-\frac{1}{k}\right) \cdot \left(\frac{l_i}{m_j}\right)$
Lognormal: proportional spread	$\frac{1}{l_i} \exp\left(\mu_1 + \log\left(\frac{m_j}{m_1}\right) - \left(\frac{\sigma^2}{2}\right) - \frac{\left(\log(l_i) - \mu_1 - \log\left(\frac{m_j}{m_1}\right)\right)^2}{2\sigma^2}\right)$	$\frac{1}{\sigma^2} \cdot \left(\log(l_i) \cdot \log\left(\frac{m_j}{m_1}\right) - \frac{1}{2}\log^2\left(\frac{m_j}{m_1}\right)\right) + \left(1 - \frac{\mu_1}{\sigma^2}\right) \cdot \left(\log\left(\frac{m_j}{m_1}\right)\right)$

Table 3

Equations used to estimate the modal length of blacktip sharks (*Carcharhinus limbatus*) caught with each gillnet mesh size (m_j) for all four gillnet selectivity models.

Model	Mode
Normal (fixed and proportional spread)	Mode $(m_j) = k \cdot m_j$
Gamma	Mode $(m_j) = (\alpha - 1) \cdot k \cdot m_j$
Lognormal	Mode $(m_j) = \exp(\mu - \sigma^2) \cdot \left(\frac{m_j}{m_1}\right)$

where *factor*(l_i) indicates that length class is fitted as a factor of the model, and $f_1(m_j, j)$ and $f_2(m_j, j)$ are the selectivity functions of m_j and j (right hand column of Table 2). When p_j is assumed to be proportional to mesh size ($\log p_j = \log m_j$), the form of the log-linear model is as follows:

$$\log(v_{ij}) = \log(m_j) + factor(l_i) + \beta_1 \cdot f_1(m_j, j) + \beta_2 \cdot f_2(m_j, j). \quad (3)$$

The parameters β_1 and β_2 are related to the form of the selectivity curve and are defined in Table 2. The following assumptions were made for all models: 1) catches were independent; and 2) gillnet panels were fished with equal effort. The mode, or maximum selected size for each panel, was calculated according to equations listed in Table 3. All models were fitted to the data twice, once under the assumption of equal fishing intensity and again under the assumption of fishing intensity proportional to mesh size. Overdispersion, or lack of fit, was tested by calculating the dispersion parameter, which is the model deviance divided by the degrees of freedom. When the dispersion parameter is >1, data are considered to be overdispersed.

Results

A total of 1720 blacktip sharks were measured from 1994 through 2010 (Table 4). Blacktip sharks were collected during 14 of the 17 years of the survey. Average net soak time was 2.67 hr (range: 0.17–23.83 hr) over 1573 sets. Some outliers were excluded when sampling protocol was considered to be out of the ordinary procedure. The majority (97%) of blacktip sharks caught in all panels were immature and less than 110 cm FL (mode=65 cm FL, Fig. 2). There was a general increase in the mean size of blacktip sharks with increasing mesh size. For the panels that were fished concurrently for all years (8.9–14.0 cm mesh), the total sample sizes of measured sharks were similar (Table 4).

Table 4

Length distribution for all blacktip sharks (*Carcharhinus limbatus*) caught in each gillnet mesh panel in the Gulf of Mexico Shark Pupping and Nursery (GULFSPAN) Survey in northwest Florida, 1994–2010.

Fork length (cm)	Mesh sizes (cm)						
	7.6	8.9	10.2	11.4	12.7	14.0	20.3
42.5	4	4	4	0	1	0	0
47.5	2	10	14	18	6	4	0
52.5	13	25	29	57	21	22	2
57.5	13	20	32	53	30	43	3
62.5	12	24	21	41	63	41	0
67.5	7	30	31	29	47	31	4
72.5	6	26	30	34	20	32	6
77.5	13	36	34	21	30	20	5
82.5	8	15	20	22	17	28	7
87.5	4	29	24	34	25	16	9
92.5	7	15	17	20	14	15	9
97.5	0	14	12	15	13	14	18
102.5	2	4	16	15	9	8	17
107.5	0	10	5	1	5	4	12
112.5	0	1	0	2	4	0	6
117.5	0	2	0	4	3	0	8
122.5	0	2	1	1	0	0	4
127.5	0	0	0	1	0	0	2
132.5	0	0	0	0	0	0	0
137.5	0	0	0	0	0	0	2
142.5	0	0	0	1	0	0	1
147.5	1	0	1	0	0	0	0
Totals	92	267	291	369	308	278	115

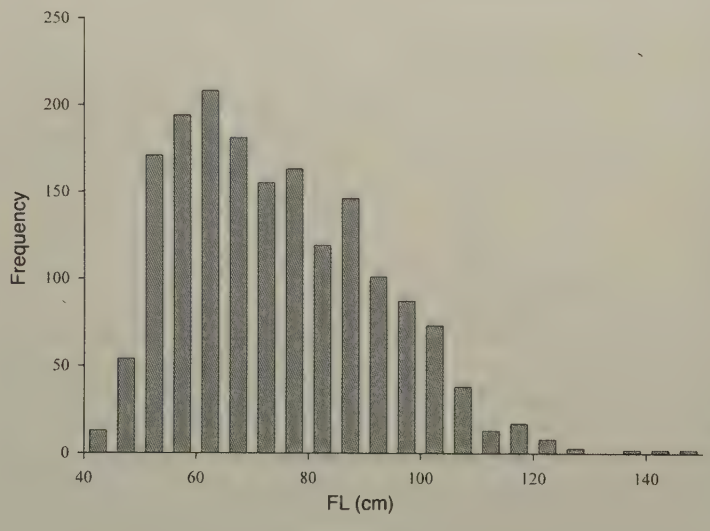

Figure 2

Length frequency of blacktip sharks (*Carcharhinus limbatus*) in fork length (FL) for all years combined caught in the Gulf of Mexico Shark Pupping and Nursery (GULFSPAN) survey in northwest Florida, 1994–2010.

The normal, fixed-spread models had the lowest model deviance overall, with the model incorporating fishing intensity proportional to mesh size having the lowest total model deviance (Fig. 3, Table 5). The ratio of model deviance to degrees of freedom was higher than 1 (2.9), indicating overdispersion of the data. This result indicates that blacktip sharks may not have behaved independently (e.g., with schooling behavior), violating the first assumption of independent catches. Residual plots showed a similar degree of bias for all models (Fig. 3), with none demonstrating markedly different fits to the data. The biggest difference among models was for the largest mesh (20.3 cm) for which the normal (proportional spread), lognormal, and gamma curves under-represented some of the smaller length classes. The highest number of positive residuals was seen for the smaller length classes (50–70 cm FL) in mesh sizes 11.4 cm and 12.7 cm and, to a lesser degree, the 14.0 cm panel for all models (Fig. 3). The plots indicated that more of the smaller individuals were caught in these panels than predicted by the models. The largest and smallest mesh sizes (20.3 and 7.6 cm) caught fewer of the smallest sharks than predicted by the models. The residuals did not indicate systematic bias in any of the models aside from the lack of fit to the smallest size classes (Fig. 3). Predicted selectivity curves for the normal, fixed-spread model assuming proportional fishing intensity plotted with observed length-frequencies for each mesh size (Fig. 4) showed that the model fitted the observed data well.

Discussion

In previous gillnet selectivity studies on sharks, a gamma-shaped distribution has been assumed (Carlson and Cortes, 2003; Kirkwood and Walker, 1986; McLoughlin and Stevens, 1994; Simpfendorfer and Unsworth, 1998), based on the specialized SELECT method described by Kirkwood and Walker (1986). However, a more recent study on the gillnet selectivity for sandbar sharks *C. plumbeus* (McAuley et al., 2007) found that all four models estimated by the Millar and Holst (1997) method provided better fits than the Kirkwood and Walker (1986) gamma model. Our study on blacktip sharks indicated that the normal, fixed spread models provided the best fit. A more limited study in North Carolina (Thorpe and Frierson, 2009) found that the normal model with spread proportional to mesh size generally provided the best fit for blacknose (*C. acronotus*), bonnethead (*Sphyrna tiburo*), and blacktip sharks. Although the method of Kirkwood and Walker (1986) was not employed in this study, the gamma curve estimated by the Millar and Holst (1997) SELECT method provided a poorer fit than the normal and lognormal models. Therefore, it

Table 5

Gillnet selectivity parameter estimates for each model for blacktip sharks (*Carcharhinus limbatus*) in northwest Florida, 1994–2010. All four models were run twice: first assuming fishing intensity to be equal across mesh sizes and again assuming that fishing intensity was proportional to mesh size. Model deviance is the likelihood ratio goodness of fit, with 130 degrees of freedom for each model.

	Equal fishing intensity		Proportional fishing intensity	
Model	Parameters	Model deviance	Parameters	Model deviance
Normal (fixed spread)	$(k, \sigma)=(5.98, 30.98)$	411.79	$(k, \sigma)=(6.94, 34.91)$	371.36
Normal (prop. spread)	$(a_1, a_2)=(6.80, 10.11)$	536.33	$(a_1, a_2)=(8.11, 8.20)$	553.73
Lognormal	$(\mu_1, \sigma)=(4.00, 0.41)$	440.33	$(\mu_1, \sigma)=(4.17, 0.41)$	440.33
Gamma	$(\alpha, k)=(6.39, 1.17)$	469.68	$(\alpha, k)=(7.39, 1.17)$	469.68

was not necessary to test a separate method to estimate a gamma selectivity curve.

Residual plots from all selectivity models showed some degree of bias for the smaller (50–70 cm FL) size classes in the 11.4-, 12.7-, and 14.0-cm mesh sizes. This finding indicated that all models underestimated the numbers of small blacktip sharks caught in these mesh sizes, and these underestimates could be an artifact of the sampling design of the GULFSPAN juvenile shark survey (Carlson and Brusher, 1999). In this survey gillnet panels were arranged in increasing order by mesh size, and the order of panels was not randomized. Randomization of gillnet panels is common in selectivity experiments because it is thought to reduce the potential preference of fish for any one area of the net. However, because fixed stations were not used, and the nets were fished at a variety of depths, habitats, and seasons, sampling design was probably not a factor in the model's lack of fit to the data. The overdispersion of the data could be a result of the pooling of the data into 5-cm bins, or could indicate schooling behavior by some size classes of blacktip sharks. Shark species are known to segregate by size and sex; therefore the capture of a cluster of similar-size blacktip sharks is likely. Overdispersion does not necessarily affect parameter estimation (Millar and Fryer, 1999), although an initial model assumption may have been violated.

Although the assumption of equal catches may have been violated, the second assumption of equal fishing effort among gillnet panels was most likely met. The shallow bays and estuaries sampled, along with the length of the net (~600 m), decreased the probability of different panels fishing in different habitats and depth zones. Commercial gear can be several kilometers in length, and sagging can cause the middle part of the gear to fish in different depth strata than those at the ends. Blacktip sharks were therefore equally likely to encounter each panel of the GULFSPAN survey gillnet.

On occasion, adult blacktip sharks (>130 cm FL) have been captured in the survey areas on longlines (Bethea and Carlson[3]). However, larger sharks are less likely to be caught in gillnets with mesh sizes smaller than 20 cm, and those few large sharks captured in the smaller mesh sizes were generally entangled by rolling in the gear—a phenomenon that was also noted for finetooth sharks (*C. isodon*) (Carlson and Cortes, 2003). All gillnet panels, except the 20.3 cm panel, were monofilament, and large sharks were able to break the monofilament and escape the gear. Such cases where larger sharks were entangled in smaller mesh sizes or where they broke free of the net could also have affected the lack of fit because the assumption of geometric similarity would not stand. The occurrence of larger sharks in small mesh sizes may have been reflected by the high model deviances for the models (normal proportional spread, lognormal, and gamma) where geometric similarity of the data was assumed. However, other than the lack of fit to the smallest size classes, the models described the data very well, with residuals showing mostly equal error distribution and little systematic bias.

Because of the change in the gear from 2005 through 2006, several attempts were made to account for a year effect within the SELECT method. Because of low sample sizes within years, especially for the 7.6- and 20.3-cm panels, it was not possible to incorporate year as a factor. For instance, a total of 92 and 115 blacktip sharks were captured by the 7.6- and 20.3-cm panels, respectively. Although these sample sizes were adequate for the overall model, when broken down by year the sample sizes were in the single digits for most size classes. The data were also separated into two time periods (1994–2005 and 2006–10), and the SELECT method was used to estimate selectivity models for each time period. The first time period produced reasonable results; however, no realistic solution was found for the second time period. This could also be due to sample sizes in the second time period. Although

[3]Dana M. Bethea and John. K. Carlson. 2011. Unpubl. data. Panama City Laboratory, Southeast Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 3500 Delwood Beach Rd., Panama City, Florida 32408.

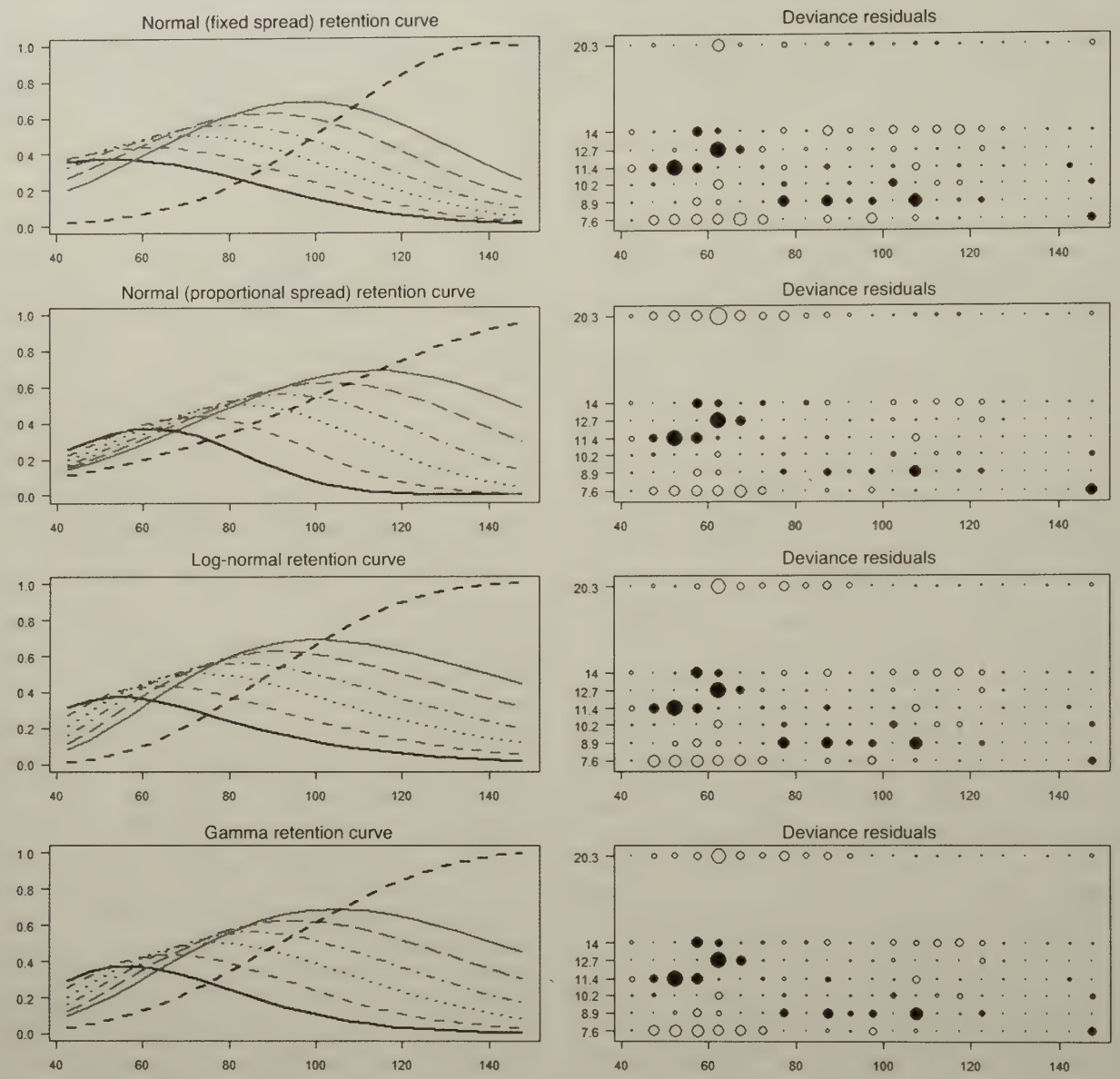

Figure 3

Gillnet selectivity curves and residuals estimated for blacktip sharks (*Carcharhinus limbatus*) in the Gulf of Mexico Shark Pupping and Nursery (GULFSPAN) survey in northwest Florida calculated from the normal (fixed spread), normal (proportional spread), lognormal, and gamma distributions. The plots on the left are the estimated gillnet selectivity curves with relative retention probability on the *y* axis. Increasing height of the curves indicates increasing mesh sizes. The plots on the right show the residuals of the models and mesh size on the *y* axis increases from bottom to top. Filled circles represent positive residuals and open circles represent negative residuals. The area of the circle is proportional to the square of the residual.

there may have been a year effect that we were unable to account for, this is unlikely because of the nature of the survey and the species studied. Generally, year-to-year variability in recruitment is lower in sharks than in teleosts because of the production of large, well-developed young and low natural mortality (Smith et al., 1998; Walker, 1998). The GULFSPAN survey primarily targets juvenile sharks in nursery areas, and the majority of the blacktip sharks captured were juveniles. Therefore it is probable that interannual size variability was low in the survey area for blacktip sharks. Although this is an important factor that could be applied to other selectivity studies with more robust sample sizes, current stock assessment models

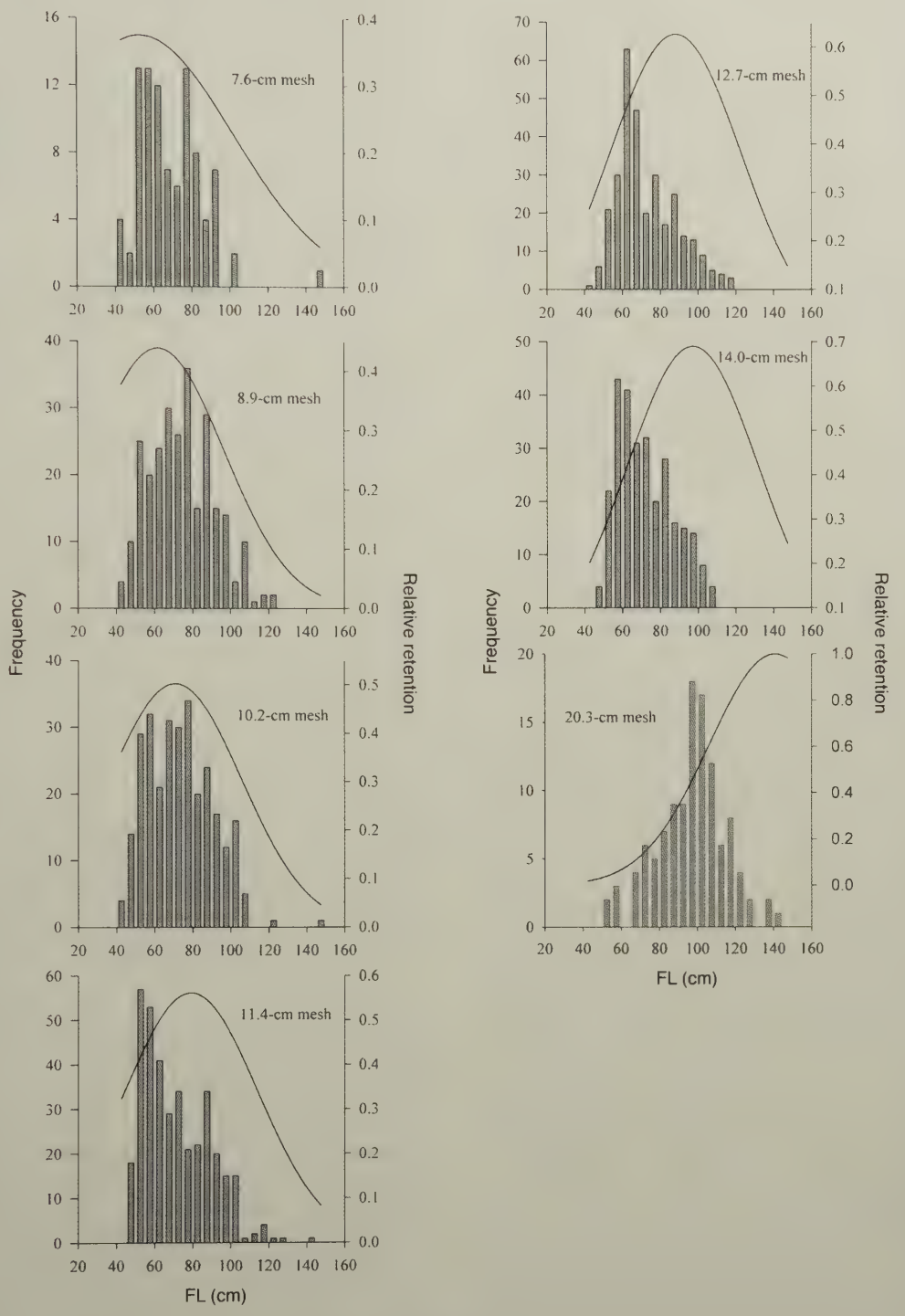

Figure 4

Selectivity curves for the normal proportional spread model where fishing intensity is assumed to be proportional to mesh size. Curves were plotted with observed data on frequency of fork lengths (FL) for blacktip sharks (*Carcharhinus limbatus*) caught in the Gulf of Mexico Shark Pupping and Nursery (GULFSPAN) survey. Selectivity curves and length frequencies are plotted separately by mesh size. Relative retention is the probability that a fish of a given length class that comes into contact with that mesh size is captured.

Table 6

Mode estimates (maximum selectivity) for blacktip sharks (*Carcharhinus limbatus*) (FL cm) caught in gillnets in northwest Florida for each mesh size fished and selectivity model. All four models were run twice: first assuming fishing intensity to be equal across mesh sizes and again assuming that fishing intensity was proportional to mesh size. Numbers in parentheses represent standard deviations, calculated for each mesh size when applicable. The normal, fixed spread and lognormal standard deviations are constant for all mesh sizes.

	Modes of selectivity curves						
Mesh size (cm)	7.6	8.9	10.2	11.4	12.7	14.0	20.3
Equal fishing intensity							
Normal: fixed spread	45.44 (30.98)	53.22	60.99	68.16	75.94	83.71	121.38
Normal: prop. spread	51.65 (24.16)	60.49 (28.30)	69.32 (32.43)	77.48 (36.24)	86.31 (40.38)	95.15 (44.51)	137.96 (64.54)
Gamma	47.86 (22.44)	56.05 (26.28)	64.24 (30.11)	71.79 (33.66)	79.98 (37.49)	88.17 (41.33)	127.84 (59.93)
Lognormal	45.88 (25.59)	53.73	61.58	68.83	76.68	84.52	122.56
Proportional fishing intensity							
Normal: fixed spread	52.78 (34.91)	61.81	70.84	79.18	88.21	97.23	140.99
Normal: prop. spread	61.64 (21.76)	72.18 (25.48)	82.73 (29.20)	92.46 (32.64)	103.00 (36.36)	113.55 (40.08)	164.65 (58.12)
Gamma	56.74 (24.13)	66.44 (28.26)	76.15 (32.38)	85.10 (36.19)	94.81 (40.32)	104.51 (44.45)	151.54 (64.45)
Lognormal	54.43 (30.36)	63.74	73.06	81.65	90.96	100.27	145.40

for sharks do not include year-specific selectivity functions (SEDAR, 2006).

Gillnet selectivity is more highly influenced by morphological features such as girth and the presence or absence of hard structures than it is by the length of a fish (Reis and Pawson, 1999; Carol and García Berthou, 2007). Nevertheless, straight-line measured length can often be used as a proxy for girth in selectivity studies because of the close direct relationship between the two parameters (Reis and Pawson, 1999), with exceptions for cases of unusual morphological features (e.g., in hammerheads [Thorpe and Frierson, 2009]) or behavioral response to entanglement (e.g., finetooth sharks [Carlson and Cortes, 2003]). Many sharks in the family Carcharhinidae share similar body shape and structure (Compagno and Niem, 1998), with girth and the rigidity of fins acting as a limiting factor for capture by gillnets (Carlson and Cortes, 2003; McAuley et al., 2007). Girth-to-length relationships have been found to be similar among related species of sharks (McLoughlin and Stevens, 1994). It is therefore possible that selectivity curves could be family-specific rather than species-specific for sharks. The most recent data have shown that the normal selectivity curves may provide the best fit for sharks in the family Carcharhinidae (McAuley et al., 2007; Thorpe and Frierson, 2009), indicating that the results for blacktip sharks could be useful for other carcharhinids of similar size. Selectivity parameters estimated for the blacktip shark could be used as a proxy for other species in the same family when species-specific selectivity estimates are unavailable. This theory could be tested by applying this method to other similar-size shark species for which a gillnet selectivity curve has been estimated, and should be pursued further as more data become available.

Thorpe and Frierson (2009) found length modes of 97 and 88 cm FL for blacktip sharks caught in mesh sizes 7.6 and 10.2 cm, respectively, whereas we estimated modes of 46 and 62 cm FL for the same mesh sizes (Table 6). However, Thorpe and Frierson (2009) failed to fit a selectivity curve to the individual mesh sizes because of the wide spread of the sparse length data. Their study was based on a small number of samples (n=76) and the modes for only two mesh sizes were estimated. The low sample size reported by Thorpe and Frierson (2009) was likely due to the relatively short duration of sampling, which was conducted over a period of eight months. Additionally, Thorpe and Frierson (2009) conducted their survey more than 1 km from shore, where the likelihood of small juveniles coming in contact with the gear was low. Total effort was not reported; however, catch rates were low in all gillnet panels (<0.15 blacktip sharks caught per hour of fishing). It is also possible that the size classes sampled in both studies were not reflective of the true size structure of the population because localized concentrations of sharks in each area that were available to the gear probably differed. The true availability of blacktip sharks to gillnets in different regions cannot be known; therefore applying selectivity functions should

be done with a proper context and with supporting length-frequency data when possible.

Based on data from fisheries observers, the average mesh size used from 2005 through 2010 in the commercial anchored gillnet fishery in the U.S. Atlantic Ocean was 11.1 cm, with a range of 8.5–16.0 cm (Passerotti[4]). The modal length calculated by using the equation in Table 3 for normal models indicates that blacktip sharks approximately 77 cm FL should be most vulnerable to the average mesh size in the commercial gillnet fishery. When calculated by using the full range of mesh sizes, the predicted modes range from 59 to 111 cm FL. Average lengths of blacktip sharks measured by observers captured by commercial anchored gillnets from 2005–2010 ranged from 79 to 107 cm FL (Baremore et al., 2007; Passerotti and Carlson, 2009, 2010; Passerotti et al., 2010, 2011). The observed lengths are consistent with the selectivity model estimated for blacktip sharks. Blacktip sharks are born at approximately 40 cm FL and mature between 120 and 130 cm FL (5–7 yr) in the U.S. Atlantic Ocean (Carlson et al., 2006), suggesting that the blacktip sharks most vulnerable to commercial gear are juveniles. Juvenile blacktip sharks use inshore nursery areas during spring and summer months, but migrate into deeper waters in the fall and winter (Castro, 1993; Heupel et al., 2007). Commercial gillnet fishermen operating in states with gillnet bans are required to fish at least 4.8 km from shore (federal waters) in the U.S. Atlantic Ocean; therefore the smallest juvenile blacktip sharks may not be as vulnerable to bycatch in these areas, especially during summer months. However, in states such as North Carolina, which allow commercial gillnet fishing in state waters, the potential for gear interaction with juvenile blacktip sharks year-round is higher. Observer data show that blacktip sharks <120 cm FL are captured in commercial gillnet fisheries and therefore juvenile blacktip sharks are likely affected by both offshore and inshore gillnet fisheries.

Thorpe and Frierson (2009) reported a mortality rate of 90.5% for blacktip sharks captured in experimental gillnets. Although soak time was not reported, the gillnets and sampling protocol in their study were designed to mimic those commonly used by commercial gillnet fishermen in North Carolina; therefore it is probable that juvenile blacktip sharks interacting with commercial gillnets may also experience high bycatch mortality. Demographic evidence suggests that population growth rates are more sensitive to survival of juvenile life stages of sharks than adults (Cortés, 2002). Therefore, modeling of the gear selectivity of gillnet fisheries, and particularly modeling bycatch from fisheries that have the potential to impact juveniles, is especially important.

Blacktip sharks are a commercially exploited species in U.S. waters, and the stock status in the Atlantic Ocean and Gulf of Mexico is assessed by the National Marine Fisheries Service on a regular basis (NMFS, 2002; SEDAR, 2006). Bycatch estimates for blacktip sharks are available from observer data (Passerotti et al., 2010), and fishing intensity of the Spanish and king mackerel gillnet fisheries has been previously estimated (SEDAR 2008; 2009). These fishery-dependent data, along with selectivity curves provided by this study, can be used by assessment scientists to estimate the selectivity of blacktip sharks caught as bycatch by commercial gillnet fisheries in the U.S. Atlantic Ocean. Bycatch data are equally as important as primary catch data for stock assessment models (NMFS[5]; SEDAR, 2006), though often more difficult to attain because bycatch is generally discarded at sea. This study provides valuable information for assessment scientists and managers tasked with estimating the size structure of blacktip sharks caught by commercial gillnet fisheries.

Conclusions

Juvenile blacktip sharks are caught as bycatch in commercial gillnet fisheries in the U.S. Atlantic Ocean, although the impact on the population has not been assessed. The results from this study showed that gillnet selectivity for juvenile blacktip sharks caught in the fishery-independent survey was best described by a normal selectivity curve with fixed spread and with fishing intensity proportional to mesh size. Because many commercial gillnet fisheries use mesh sizes similar to those used to produce these results, it may be possible to estimate the length frequencies of juvenile blacktip sharks influenced by these coastal fisheries. Selectivity estimates may also be applicable to other sharks of similar size for which species-specific information is unavailable. Future studies should focus on fishery-dependent gillnet selectivity estimates to determine if selectivity changes with gear, location, or target species.

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[4] Passerotti, M. 2011. Personal commun. Panama City Laboratory, Southeast Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 3500 Delwood Beach Rd., Panama City, Florida 32408.

[5] NMFS (National Marine Fisheries Service). 2002. Stock assessment of large coastal sharks in the U.S. Atlantic Ocean and Gulf of Mexico: final meeting report of the 2002 shark evaluation workshop. Contribution report 02-03-177, 64 p. Sustainable Fisheries Div., National Marine Fisheries Service, NOAA, Silver Spring, MD.

information on commercial gillnet fisheries. The comments of three anonymous reviewers also added to the overall quality of the article. Sharks were collected under Florida Fish & Wildlife Conservation Commission special activity licenses 02R-075, 03SR-075A, 04SR-075 and 08SR-075.

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Population structure of pink salmon (*Oncorhynchus gorbuscha*) in British Columbia and Washington, determined with microsatellites

Terry D. Beacham (contact author)[1]
Brenda McIntosh[1]
Cathy MacConnachie[1]
Brian Spilsted[2]
Bruce A. White[3]

E-mail address for contact author: Terry.Beacham@dfo-mpo.gc.c

[1] Fisheries and Oceans Canada
Pacific Biological Station
3190 Hammond Bay Road
Nanaimo, B. C., Canada V9T 6N7

[2] Fisheries and Oceans Canada
417-2nd Avenue West
Prince Rupert, B. C. Canada V8J 1G8

[3] Pacific Salmon Commission
600-1155 Robson Street
Vancouver, B. C., Canada V6E 1B5

Abstract—Population structure of pink salmon (*Oncorhynchus gorbuscha*) from British Columbia and Washington was examined with a survey of microsatellite variation to describe the distribution of genetic variation. Variation at 16 microsatellite loci was surveyed for approximately 46,500 pink salmon sampled from 146 locations in the odd-year broodline and from 116 locations in the even-year broodline. An index of genetic differentiation, F_{ST}, over all populations and loci in the odd-year broodline was 0.005, with individual locus values ranging from 0.002 to 0.025. Population differentiation was less in the even-year broodline, with a F_{ST} value of 0.002 over all loci, and with individual locus values ranging from 0.001 to 0.005. Greater genetic diversity was observed in the odd-year broodline. Differentiation in pink salmon allele frequencies between broodlines was approximately 5.5 times greater than regional differentiation within broodlines. A regional structuring of populations was the general pattern observed, and a greater regional structure in the odd-year broodline than in the even-year broodline. The geographic distribution of microsatellite variation in populations of pink salmon likely reflects a distribution of broodlines from separate refuges after the last glaciation period.

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Pink salmon (*Oncorhynchus gorbuscha*) spawn in more than 700 rivers in British Columbia (Aro and Shepard, 1967), and the distribution of spawning populations varies in odd-numbered years and even-numbered years. Spawning occurs primarily only in odd years in the Fraser River drainage, mainly in even years on the Queen Charlotte Islands, and in both years in central and northern coastal areas of British Columbia (Neave, 1952). Because virtually all pink salmon mature at two years of age (Bilton and Ricker, 1965), two distinct broodlines in the species have developed (odd-year and even-year), with virtually no gene flow between the broodlines. This reproductive isolation of the broodlines has resulted in reported differences in body size (Godfrey, 1959), morphological characteristics (Ricker, 1972; Beacham, 1985), timing of spawning (Aro and Shepard, 1967; Dyagilev and Markevich, 1979), and genetic differentiation (Aspinwall, 1974; Beacham et al., 1988). Evaluation of the genetic population structure both between and within broodlines in British Columbia and Washington form the basis of the current study.

Estimation of genetic population structure has been a key area of research in salmon assessment and management. Identification of a genetically distinct group of populations in the distribution of a species is a key step in conserving and maintaining genetic diversity. Genetically distinct populations or regional groups of populations (stocks) were determined through surveys of genetic variation to evaluate the population structure of a species (Shaklee and Bentzen, 1998). Identification of genetically distinct groups in the distribution of pink salmon in British Columbia and Puget Sound may lead to the conservation of genetic diversity by fisheries and resource management. An evaluation of genetic variation is effective in describing the population structure of salmonids, is a key part in the elucidation of management units or conservation units for a species and can be applied to manage fisheries exploiting specific stocks of salmon.

Determination of genetic population structure is an important part in developing a genetically based method for estimation of stock composition. Allozymes were initially the key set of genetic markers used in evaluat-

ing population structure in pink salmon in British Columbia (Beacham et al., 1988; Shaklee et al., 1991) and elsewhere in the Pacific Rim distribution of the species (Aspinwall, 1974; Varnavskaya and Beacham, 1992; Shaklee and Varnavskaya, 1994; Noll et al., 2001; Hawkins et al., 2002). Analysis of allozyme variation provided the general pattern of marked differentiation between the broodlines, but identification of fine-scale regional structure was limited, although estimation of stock composition of samples from mixed-stock fisheries was conducted (Beacham et al., 1985; Shaklee et al., 1991). Development of DNA markers has led to new avenues of research for using genetic variation in defining population structure. Mitochondrial DNA variation again showed strong differentiation between the broodlines, but differentiation among regional groups of pink salmon was limited (Brykov et al., 1996, 1999; Churikov and Gharrett, 2002). However, Golovanov et al. (2009) noted that differentiation among even-year populations was higher than among odd-year populations in the northern Sea of Okhotsk region.

Microsatellites are reported to be useful for evaluating fine-scale population structure in salmonids (Banks et al., 2000) and have been used to evaluate large-scale and regional variation in chum salmon (*O. keta*) (Beacham et al., 2009). Initial applications of microsatellite variation to evaluate individual identification and population structure were reported by Olsen et al. (1998, 2000a). However, surveys of population variation were quite limited in these studies, and no comprehensive evaluation of variation at microsatellites has been conducted for pink salmon. A survey of microsatellite variation over a broader geographic range of pink salmon distribution would likely be valuable for evaluating population structure.

In the current study, we outline the microsatellite-based population structure of pink salmon in British Columbia and Washington as an initial step in evaluating whether higher resolution in estimation of stock composition may be possible when compared with estimates previously derived with allozymes. This objective was accomplished by analyzing variation at 16 microsatellite loci to evaluate relationships in population structure of pink salmon, as well as by analyzing regional differences in allelic variation. The distribution of genetic diversity among broodlines, regions, and populations was estimated in the study, as well as the stability of population structure.

Materials and methods

Collection of DNA samples and laboratory analysis

Tissue samples were collected from mature pink salmon. Samples were preserved in 95% ethanol, and sent to the Molecular Genetics Laboratory at the Pacific Biological Station of Fisheries and Oceans Canada. DNA was extracted from the tissue samples by using a variety of methods, including a chelex resin protocol outlined by Small et al. (1998), a Qiagen 96-well DNeasy®[1] procedure (Qiagen, Mississauga, Ontario), or a Promega Wizard SV96 Genomic DNA Purification system (Promega, Madison, WI). Once extracted DNA was available, surveys of variation at 16 microsatellite loci were conducted: *Oki10* (Smith et al., 1998), *Oki101* (Beacham et al., 2011), *OtsG68*, *OtsG253b*, *OtsG311* (Williamson et al., 2002), *Ots213* (Greig et al., 2003), Ots7e (Wright et al., 2008), *One101*, *One102*, *One104*, *One109*, *One111*, *One114* (Olsen et al., 2000b), *Ssa407*, *Ssa408*, *Ssa419* (Cairney et al., 2000)

Table 1

Microsatellite loci surveyed in pink salmon (*Oncorhynchus gorbuscha*) and their associated annealing and extension temperatures and times (seconds), as well as the number of cycles used in polymerase chain reaction amplifications.

Locus	Annealing	Extension	Cycles
Oki10	53°C/30s	70°C/30s	39
Oki101	53°C/45s	68°C/30s	40
One101	50°C/30s	70°C/30s	39
One102	50°C/30s	70°C/30s	39
One104	50°C/30s	70°C/30s	36
One109	55°C/30s	70°C/30s	34
One111	55°C/30s	70°C/30s	34
One114	50°C/30s	70°C/45s	38
Ots213	52°C/45s	72°C/60s	38
Ots7e	51°C/30s	72°C/30s	35
OtsG253b	60°C/45s	72°C/45s	35
OtsG311	50°C/45s	68°C/45s	34
OtsG68	50°C/30s	70°C/30s	36
Ssa407	60°C/30s	70°C/30s	39
Ssa408	60°C/45s	70°C/45s	40
Ssa419	50°C/30s	70°C/30s	40

In general, polymerase chain reaction (PCR) DNA amplifications were conducted by using a DNA Engine Cycler Tetrad2 (BioRad, Hercules, CA) in 6-µL volumes consisting of 0.15 units of Taq polymerase, 1-µL of extracted DNA, 1×PCR buffer (Qiagen), 60 µM each nucleotide, 0.40 µM of each primer, and deionized water. The thermal cycling profile involved one cycle of Taq activation for 15 minutes at 95°C, followed by a denaturation cycle of 30 seconds at 94°C, with annealing and extension conditions for each locus as outlined in Table 1. PCR fragments were initially size fractionated in denaturing polyacrylamide gels with an ABI 377 automated DNA sequencer, and genotypes were scored by Genotyper, vers. 2.5 software (Applied Biosystems, Foster City, CA) by using an internal lane sizing standard. Later in the study, microsatellites were size fractionated in an ABI 3730 capillary DNA sequencer, and

[1] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 2

Pink salmon (*Oncorhynchus gorbuscha*) spawning regions, number of populations sampled, years when sampling occurred, average number of fish sampled per population per year over all populations within a region, and average total number of fish sampled (N) per population within the region for 146 odd-year and 116 even-year populations in 15 geographic regions (Fig. 2). Listing of populations in each region as well as allele frequencies for all population samples surveyed in this study are available at the Molecular Genetics Laboratory website http://www.pac.dfo-mpo.gc.ca/science/facilities-installations/pbs-sbp/mgl-lgm/data-donnees/index-eng.htm. Values shown are averages with the ranges of samples sizes in parentheses.

Region	Populations	Years	Average annual population sample size	Average population size (N)
Washington (odd)	12	1995–2009	110 (44–498)	257 (98–755)
Fraser River-upper (odd)	9	1987–2009	95 (69–102)	201 (100–463)
Fraser River-lower (odd)	6	1987–2009	87 (50–100)	245 (98–463)
East Coast Vancouver Island (odd)	10	1987–2009	108 (85–219)	173 (85–397)
South Coast British Columbia (odd)	13	1987–2009	105 (25–200)	169 (38–390)
Central Coast British Columbia (odd)	59	2003–2009	111 (2–227)	164 (32–394)
Skeena River (odd)	10	2003–2007	163 (67–229)	228 (123–393)
North Coast British Columbia (odd)	25	2003–2009	151 (9–233)	211 (87–381)
Queen Charlotte Islands (odd)	2	2005	210 (200–219)	210 (200–219)
East Coast Vancouver Island (even)	2	2006–2008	83 (50–113)	124 (85–163)
South Coast British Columbia (even)	11	2002–2010	119 (27–237)	162 (47–452)
Central Coast British Columbia (even)	50	2002–2010	96 (5–202)	133 (18–312)
Skeena River (even)	7	2002–2006	162 (63–228)	208 (100–381)
North Coast British Columbia (even)	25	2002–2010	113 (3–215)	190 (24–425)
Queen Charlotte Islands (even)	21	2002–2006	135 (32–200)	176 (32–364)

genotypes were scored by GeneMapper software, vers. 3.0 (Applied Biosystems) by using an internal lane sizing standard. Allele identification between the two sequencers was standardized by analyzing approximately 600 individuals on both platforms and converting the sizing in the gel-based data set to match that obtained from the capillary-based set.

Data analysis

All annual samples available for a location were combined to estimate population allele frequencies, as is recommended by Waples (1990). Each population in each broodline at each locus was tested for departure from Hardy-Weinberg equilibrium of genotypic frequencies by using the software Genetic Data Analysis (GDA; Univ. of Connecticut, Storrs, CT). Critical significance levels for simultaneous tests were evaluated by using Bonferroni adjustment for each broodline separately (odd-year broodline: 0.05/146=0.00034, even-year broodline 0.05/116=0.00043; Rice, 1989). Weir and Cockerham's (1984) F_{ST} estimates for each locus over all populations were calculated with FSTAT, vers. 2.9.3.2 (Goudet, 1995). The significance ($P<0.05$) of the multilocus F_{ST} value over all samples was determined by jackknifing over loci. Populations were combined into 14 regional groups in order to develop a practical method to display mean pairwise F_{ST} values between regions, as well as the mean number of alleles observed per locus in each region. These 14 regional groups were constructed from the 15 regional groups outlined in Table 2 by combining the upper and lower Fraser River regions into a single region, with other regions remaining as outlined in Table 2. Broodlines were separated in odd-year and even-year spawning lines. Geographic areas were outlined in Figure 1. The 14 regional groups correspond to the geographic areas and broodlines as follows: 1) Washington odd-year; 2) Fraser River (upper+lower) odd-year; 3) east coast Vancouver Island odd-year; 4) south coast British Columbia odd-year; 5) central coast British Columbia odd-year; 6) Skeena River odd-year; 7) north coast British Columbia odd-year; 8) Queen Charlotte Islands odd-year; 9) east cCoast Vancouver Island even-year; 10) south coast British Columbia even-year; 11) central coast British Columbia even-year; 12) Skeena River even-year; 13) north coast British Columbia even-year; 14) Queen Charlotte Islands even-year. Individual populations remained discrete within these larger regional groups for determination of pairwise F_{ST} values.

Genotypic disequilibrium and potential genetic linkage among loci were tested with GDA with 1500 iterations per test. The number of pairs of loci exhibiting potential linkage was summed for the 146 populations sampled in the odd-year broodline and 116 populations sampled in the even-year broodline (Table 2). Statistical significance was evaluated by using a Bonferroni adjustment as outlined previously.FSTAT was used to measure the "allelic richness" (allelic diversity standardized to a sample size of 240 fish per region) for the 14 regional groups of populations. Computation of the number of alleles observed per locus was carried out with GDA. Cavalli-Sforza and Edwards (CSE) chord distance (1967) was used to estimate

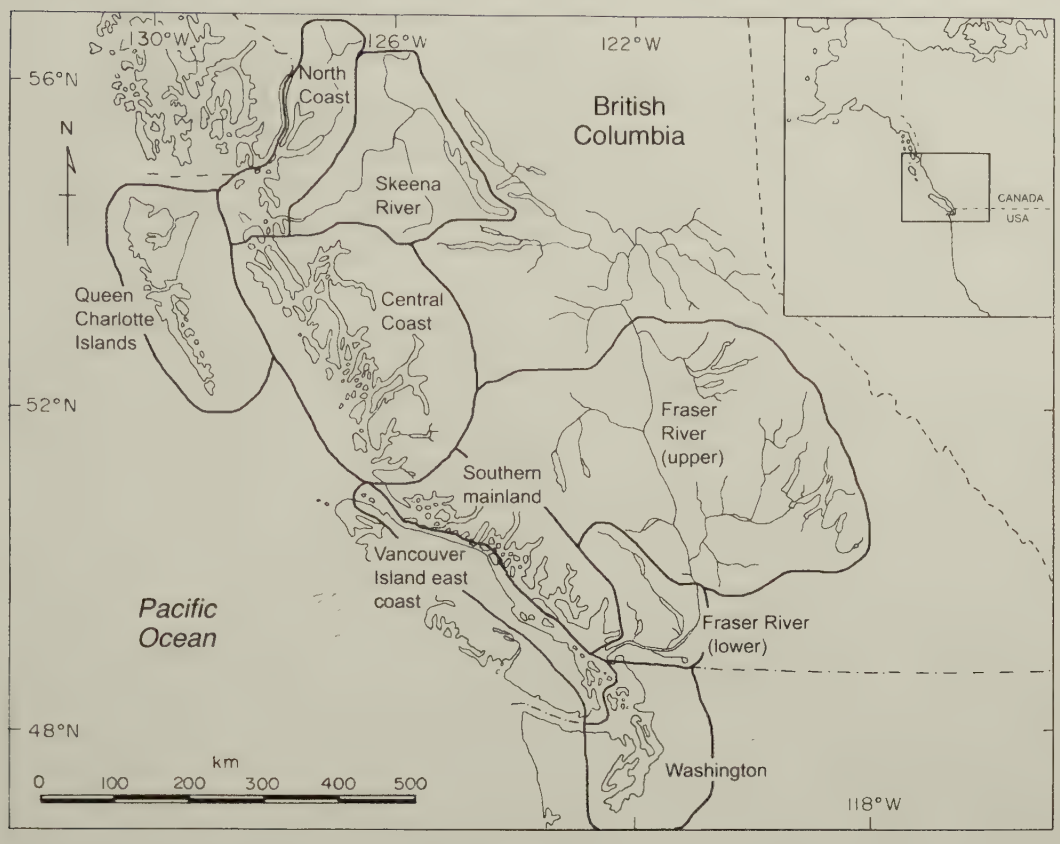

Figure 1

Map of British Columbia and northern Washington coasts indicating the general geographic regions where pink salmon (*Oncorhynchus gorbuscha*) from 146 odd-year and 116 even-year populations were surveyed, with the regions listed in Table 2. The regions depicted in the figure are the following: 1 Washington; 2 lower Fraser River; 3 upper Fraser River; 4 east coast Vancouver Island (ECVI); 5 southern British Columbia; 6 central coast; 7 Skeena River; 8 north coast; and 9 Queen Charlotte Islands. In 6 of these regions (ECVI, southern British Columbia mainland, central coast, Skeena River, north coast, Queen Charlotte Islands), pink salmon spawn in both even and odd years. Because 6 regions have both broodlines present, the map encompasses 12 regional groups of populations when even and odd populations are separated. The other 3 regional groups (upper and lower Fraser River, and Washington) have pink salmon only in odd years. This summary accounts for the 15 regional groups outlined in Table 2.

genetic distances among all populations. An unrooted neighbor-joining tree based upon CSE was generated with NJPLOT (Perriere and Gouy, 1996). Bootstrap support for the major nodes in the tree was evaluated with the CONSENSE program from PHYLIP based upon 500 replicate trees (Felsenstein, 1993). The distribution of genetic variation in pink salmon was evaluated with a gene diversity analysis with the analysis structured between broodlines, among regions within broodlines, and among populations within regions. The analysis was conducted with GDA, which will support a maximum of three nested levels of variation in addition to the error mean square. All populations outlined in Table 2 were included in the analysis. Allele frequencies for all location samples surveyed in this study are available at the Molecular Genetics Laboratory website http://www.pac.dfo-mpo.gc.ca/science/facilities-installations/pbs-sbp/mgl-lgm/data-donnees/index-eng.htm.

Results

Variation within populations

Variation was displayed in the number of observed alleles at the 16 microsatellite loci surveyed in the study. The fewest number of alleles was observed at *Ots7e* (12 alleles odd-year broodline, 13 alleles even-year broodline), and the greatest number of alleles was observed at *Oki10* (85 alleles odd-year broodline, 83 alleles even-year broodline) (Table 3). Heterozygosities were generally above 90%, with notable exceptions observed at *Ots7e* (both broodlines) and *One111* (odd-year only). Genotypic frequencies at all 16 loci surveyed typically conformed to those expected under Hardy-Weinberg equilibrium (HWE) for populations in both broodlines. Greater overall population differentiation was observed in the odd-year broodline (F_{ST} = 0.005) than in the even-year broodline (F_{ST} =0.002).

Table 3

Number of alleles per locus, an index of genetic differentiation F_{ST} (standard deviation in parentheses), expected heterozygosity (H_e), observed heterozygosity (H_o), and percent significant Hardy-Weinberg equilibrium (HWE) tests for 16 microsatellite loci among 146 odd-year and 116 even-year pink salmon (*Oncorhynchus gorbuscha*) populations.

Locus	Number of alleles	F_{ST}	H_e	H_o	HWE
Odd-year broodline					
Oki10	85	0.004 (0.000)	0.94	0.94	0.0
Oki101	83	0.002 (0.000)	0.97	0.96	0.7
One101	52	0.003 (0.000)	0.96	0.95	0.7
One102	32	0.006 (0.001)	0.92	0.91	0.0
One104	40	0.007 (0.001)	0.95	0.94	0.0
One109	32	0.005 (0.001)	0.90	0.90	0.0
One111	36	0.012 (0.001)	0.72	0.71	0.0
One114	49	0.003 (0.000)	0.96	0.95	2.1
Ots213	69	0.003 (0.001)	0.97	0.95	2.8
Ots7e	12	0.025 (0.003)	0.45	0.45	0.0
OtsG253b	46	0.005 (0.001)	0.95	0.94	1.4
OtsG311	34	0.009 (0.001)	0.89	0.88	1.4
OtsG68	34	0.004 (0.001)	0.93	0.93	0.0
Ssa407	73	0.006 (0.001)	0.94	0.94	0.0
Ssa408	69	0.002 (0.000)	0.97	0.95	6.2
Ssa419	66	0.003 (0.000)	0.96	0.93	7.5
Total		0.005 (0.001)			
Even-year broodline					
Oki10	83	0.001 (0.000)	0.94	0.93	1.8
Oki101	73	0.002 (0.000)	0.97	0.96	0.9
One101	65	0.001 (0.000)	0.96	0.95	1.8
One102	35	0.002 (0.000)	0.93	0.93	0.0
One104	36	0.004 (0.000)	0.92	0.92	0.0
One109	29	0.003 (0.000)	0.91	0.90	0.0
One111	38	0.004 (0.001)	0.92	0.91	2.6
One114	42	0.002 (0.000)	0.96	0.95	0.0
Ots213	71	0.002 (0.000)	0.97	0.97	5.1
Ots7e	13	0.005 (0.001)	0.58	0.58	1.8
OtsG253b	48	0.002 (0.000)	0.95	0.94	3.5
OtsG311	34	0.003 (0.000)	0.93	0.91	0.0
OtsG68	32	0.003 (0.000)	0.93	0.93	0.0
Ssa407	77	0.002 (0.000)	0.96	0.93	2.6
Ssa408	69	0.002 (0.000)	0.97	0.95	1.8
Ssa419	66	0.002 (0.000)	0.97	0.95	2.6
Total		0.002 (0.000)			

Individual locus F_{ST} values ranged from 0.002 to 0.012 for the odd-year broodline, and between 0.001 and 0.005 for the even-year broodline. For the odd-year broodline, individual pairs of loci displayed potential linkage of between 0% and 28% (*Ssa408* and *Ssa419*) of the populations surveyed. In the even-year broodline, individual pairs of loci displayed potential linkage of between 0% and 13% (*Ssa407* and *Ssa419*) of the populations surveyed. Potential linkage among loci was higher in the *Ssa* series of loci than that observed in the other microsatellites, but different patterns were observed within the broodlines. Potential linkage among the *Ssa* loci was not judged to be at a level that required removal from subsequent analyses.

The number of alleles observed displayed variation among the regional groups of pink salmon surveyed. With the number of alleles observed standardized to a sample size of 240 individuals per region for both broodlines, the odd-year broodline populations with the fewest number of observed alleles originated from Washington (486 alleles), whereas populations with the greatest number of alleles originated from the northern coastal region of British Columbia (551 alleles) (Table 4). In the even-year broodline, populations with the fewest numbers of alleles originated from the east

Table 4

Mean number of alleles observed per locus at 16 microsatellite loci for pink salmon (*Oncorhynchus gorbuscha*) from 14 geographic broodline areas standardized to a sample size of 240 fish per geographic area. Regional groups (see Table 2), are as follows: 1) Washington odd-year, 2) Fraser River (upper+ lower) odd-year, 3) east coast Vancouver Island odd-year, 4) south coast British Columbia odd-year, 5) central coast British Columbia odd-year, 6) Skeena River odd-year, 7) north coast British Columbia odd-year, 8) Queen Charlotte Islands odd-year, 9) east coast Vancouver Island even-year, 10) south coast British Columbia even-year, 11) central coast British Columbia even-year, 12) Skeena River even-year, 13) north coast British Columbia even-year, 14) Queen Charlotte Islands even-year. The two Fraser River regions in Table 2 were combined for the analysis.

Locus	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Odd	Even
Oki10	30.77	33.14	41.59	40.84	47.21	40.53	48.42	44.81	26.93	31.14	38.21	36.03	43.31	35.67	40.91	35.21
Oki101	50.95	53.09	54.73	55.30	55.83	51.38	54.65	55.79	49.88	48.04	51.90	52.11	55.65	48.74	53.96	51.05
One101	35.30	37.33	35.93	37.70	36.39	36.18	36.36	35.78	35.78	36.66	39.15	36.55	39.41	39.42	36.37	37.83
One102	22.73	22.25	23.22	23.45	24.44	20.79	24.40	23.99	23.94	25.73	25.53	26.08	26.16	25.68	23.16	25.52
One104	30.29	31.81	30.85	31.78	30.64	28.23	31.10	30.49	29.89	27.95	30.04	24.63	30.40	27.40	30.65	28.39
One109	17.31	18.00	17.51	19.13	19.62	20.18	20.23	18.90	16.00	18.00	18.60	18.54	19.33	16.98	18.86	17.91
One111	19.79	21.45	21.52	21.81	21.01	19.73	21.24	20.54	21.97	24.05	25.27	22.29	23.51	22.40	20.88	23.25
One114	37.24	39.89	38.61	38.84	37.30	34.99	36.19	35.26	30.00	32.23	34.74	35.46	35.78	34.58	37.29	33.80
Ots213	43.25	42.92	45.32	49.90	51.23	50.38	51.77	50.54	43.91	50.37	50.34	48.99	51.27	46.15	48.16	48.51
Ots7e	5.79	5.90	7.00	6.43	7.68	7.12	7.80	6.48	4.00	5.84	5.82	6.17	7.27	4.92	6.77	5.67
OtsG311	16.65	15.91	17.97	18.32	20.50	20.44	20.24	21.25	20.00	21.41	21.06	18.75	21.49	19.69	18.91	20.40
OtsG68	24.95	25.11	25.12	24.44	26.38	27.07	26.01	23.80	20.98	21.94	21.99	20.99	25.23	21.14	25.36	22.04
OtsG253b	33.96	33.88	34.08	35.64	33.92	31.77	34.03	32.57	32.83	34.17	35.74	34.44	36.26	33.12	33.73	34.43
Ssa407	27.87	27.35	31.41	31.74	33.37	31.83	32.28	25.33	47.90	48.86	52.42	51.36	51.01	49.25	30.15	50.13
Ssa408	52.54	53.04	54.75	51.62	52.89	49.94	54.09	52.31	49.90	48.73	54.88	52.09	55.73	51.32	52.65	52.11
Ssa419	36.33	40.19	49.00	46.13	53.07	47.58	52.36	50.93	48.00	46.94	47.97	44.46	50.95	44.42	46.95	47.12
Total	485.69	501.24	528.60	533.04	551.46	518.14	551.17	528.78	501.90	522.06	553.65	528.92	572.73	520.90	524.76	533.36

coast of Vancouver Island (502 alleles), and those populations with the greatest number of alleles originated from the northern coastal region of British Columbia (573 alleles). The greatest difference in number of alleles between the broodlines was observed at the locus *Ssa407*, with an average of 30 alleles observed at the locus in the odd-year populations, and 50 alleles observed in the even-year populations ($P<0.01$). Within the odd-year broodline, lower numbers of observed alleles of Washington populations, and to some extent Fraser River populations, compared with other regional groups of populations, were concentrated in the *Oki10* and *Ssa419* loci (Table 4).

Distribution of genetic variance

Gene diversity analysis of the 16 microsatellites surveyed was used to evaluate the distribution of genetic variation between two broodlines, among regions (15 regions, Table 2) within broodlines, and among populations within regions (146 odd-year, 116 even-year populations). The amount of variation within populations ranged from 85.1% (*One111*) to 99.8% (*Oki101*, *One101*), and averaged 98.1% across all loci (Table 5). Variation between the two broodlines accounted for 1.5% of total observed variation and was the largest source of variation after within-population variation. Variation among regions within broodlines was the next largest source of variation and accounted for 0.3% of total observed variation. Variation among populations within regions accounted for 0.2% of total observed variation. Differentiation between the broodlines was approximately three times greater than any combined regional or population source of variation. Significant broodline differentiation in allele frequencies was observed in 13 of the 16 loci surveyed, with the greatest difference observed at *One111*, which was nine times larger than that observed at any other locus (Table 5). For the geographic range of populations surveyed in the study, broodline differences contributed more to differentiation of allele frequencies than any regional or population source of differentiation.

Population structure

Regional genetic differentiation was observed among pink salmon populations sampled in the different geographic regions. As expected, the largest differences in genetic differentiation were observed between regional groups of populations when compared with populations in the alternate broodline (regional F_{ST} values ranging from 0.014 to 0.036) (Table 6). In the odd-year broodline, the largest average population differentiation was observed in comparisons of populations originating from Washington compared with populations from British Columbia (regional F_{ST} values ranging from 0.011 to 0.016) (Table 6). Within British Columbia, pink salmon in the odd-year broodline originating from the Fraser River were the most genetically distinct

Table 5

Hierarchical gene-diversity analysis of regional F_{ST} values for 262 populations of pink salmon (*Oncorhynchus gorbuscha*) within 15 regions (9 regions in odd-year broodline, 6 regions in even-year broodline) for 16 microsatellite loci, with the regions outlined in Table 2. $^{**}P<0.01$ $^{*}P<0.05$

Locus	Within populations	Among populations within regions	Among regions within broodlines	Between broodlines
Oki10	0.9967	0.0014**	0.0017**	0.0002
Oki101	0.9976	0.0013**	0.0009**	0.0002
One101	0.9976	0.0012**	0.0009**	0.0003
One102	0.9942	0.0021**	0.0023**	0.0014*
One104	0.9782	0.0021**	0.0045**	0.0152**
One109	0.9902	0.0021**	0.0025**	0.0052**
One111	0.8507	0.0022**	0.0057**	0.1414**
One114	0.9944	0.0013**	0.0013**	0.0030**
Ots213	0.9952	0.0019**	0.0012**	0.0017**
Ots7e	0.9207	0.0056**	0.0111**	0.0626**
OtsG253b	0.9955	0.0019**	0.0023**	0.0003
OtsG311	0.9772	0.0023**	0.0047**	0.0158**
OtsG68	0.9896	0.0019**	0.0020**	0.0065**
Ssa407	0.9930	0.0018**	0.0034**	0.0018*
Ssa408	0.9942	0.0013**	0.0009**	0.0036**
Ssa419	0.9949	0.0016**	0.0012**	0.0023**
Total	0.9806	0.0019**	0.0027**	0.0148**

Table 6

Mean pairwise F_{ST} values averaged over 16 microsatellite loci from 14 regional groups of pink salmon (*Oncorhynchus gorbuscha*) outlined in Table 2 that were sampled at 262 locations (146 odd-year, 116 even-year) in British Columbia and Washington. Comparisons were conducted between individual populations in each region. Values in bold on the diagonal represent comparisons among populations within each region. F_{ST} values are listed above the diagonal, and standard deviations are shown below the diagonal. RC is region code, and codes are as follows: 1) Washington odd-year, 2) Fraser River odd-year, 3) east coast Vancouver Island odd-year, 4) southern coast British Columbia odd-year, 5) central coast British Columbia odd-year, 6) Skeena River odd-year, 7) north coast British Columbia odd-year, 8) Queen Charlotte Islands odd-year, 9) east coast Vancouver Island even-year, 10) southern Coast British Columbia even-year, 11) central coast British Columbia even-year, 12) Skeena River even-year, 13) north coast British Columbia even-year, 14) Queen Charlotte Islands even-year.

RC	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	**0.011**	0.011	0.013	0.011	0.013	0.016	0.014	0.015	0.036	0.034	0.032	0.032	0.031	0.034
2	0.010	**0.001**	0.009	0.006	0.007	0.010	0.008	0.010	0.029	0.027	0.026	0.025	0.025	0.028
3	0.009	0.003	**0.006**	0.006	0.006	0.008	0.006	0.008	0.025	0.023	0.021	0.021	0.020	0.023
4	0.009	0.002	0.003	**0.004**	0.003	0.006	0.004	0.006	0.025	0.023	0.021	0.020	0.020	0.024
5	0.009	0.002	0.003	0.002	**0.001**	0.003	0.001	0.003	0.019	0.017	0.015	0.015	0.014	0.018
6	0.009	0.003	0.003	0.003	0.002	**0.001**	0.004	0.007	0.019	0.017	0.015	0.015	0.014	0.018
7	0.008	0.003	0.003	0.003	0.002	0.002	**0.001**	0.003	0.019	0.017	0.015	0.015	0.014	0.018
8	0.009	0.001	0.003	0.003	0.001	0.003	0.002	**0.003**	0.022	0.020	0.018	0.019	0.018	0.021
9	0.010	0.003	0.006	0.004	0.003	0.003	0.003	0.003	**0.008**	0.005	0.004	0.006	0.005	0.007
10	0.009	0.003	0.006	0.004	0.003	0.003	0.003	0.003	0.002	**0.003**	0.002	0.004	0.002	0.005
11	0.009	0.003	0.006	0.004	0.002	0.002	0.002	0.002	0.002	0.003	**0.001**	0.003	0.001	0.004
12	0.008	0.002	0.005	0.004	0.002	0.002	0.002	0.002	0.002	0.003	0.002	**0.002**	0.002	0.006
13	0.009	0.002	0.006	0.004	0.002	0.002	0.002	0.002	0.002	0.002	0.001	0.002	**0.001**	0.004
14	0.009	0.002	0.006	0.004	0.002	0.002	0.002	0.002	0.003	0.002	0.001	0.002	0.001	**0.002**

group of populations (regional F_{ST} values ranging from 0.006 to 0.010). The least differentiation was observed between populations from the northern and central coastal regions of British Columbia (F_{ST}=0.001). In the even-year broodline, the largest regional genetic differentiation was observed between populations from the east coast of Vancouver Island and those from the Queen Charlotte Islands (F_{ST}=0.007), whereas the least differentiation between regional groups of populations was observed between the northern and central coastal regions of British Columbia (F_{ST}=0.001) (Table 6).

Two distinct lineages of pink salmon were observed in the cluster analysis, and they were clearly based on whether pink salmon spawned in odd-numbered or even-numbered years. All odd-year populations clustered together with 100% bootstrap support, as did all even-year populations (Fig. 2). Within the odd-year broodline, a Washington group of populations was well supported (Washington populations clustered together in 83% of dendrograms evaluated). Within Washington, further geographic subdivision was observed, with populations from the Strait of Juan de Fuca (Gray Wolf River, Dungeness River) clustering with the Hood Canal hatchery population in 100% of dendrograms evaluated. The Hood Canal hatchery population was the most genetically distinct population included in the survey (Fig. 2). The three remaining populations from Hood Canal (Dosewallips River, Hamma Hamma River, and Duckabush River), in addition to the Gray Wolf River, Dungeness River, and Hood Canal hatchery populations, were well separated from other populations in Washington, clustering together in 100% of dendrograms evaluated. Pink salmon populations from the Fraser River in southern British Columbia were a well-defined geographic cluster— all 15 populations clustered together in 98% of dendrograms evaluated. Furthermore, populations in the upper portion of the drainage were separated from those populations in the lower portion of the drainage, with upper populations clustering together in 98% of dendrograms evaluated. Populations from the central portion of the east coast of Vancouver Island (Quinsam River, Puntledge River, Oyster River, Big Qualicum River, and Nanaimo River) clustered together in 100% of dendrograms evaluated, as did 98% of populations from the northern portion of the east coast of Vancouver Island (Keogh River, Quatse River, Cluxewe River). Populations from the northern portion of the South Coast of British Columbia (Kakweiken River, Lull Creek, Ahta Creek, Heydon River, Glendale River) constituted a well-defined group (96% of dendrograms evaluated). Those in the southern portion of the south coast (Cheakamus River, Ashlu River, Mamquam River, Squamish River, Indian River) were not well supported, but displayed some affinity to each other in the cluster analysis (Table 6). All 10 odd-year populations sampled from the Skeena River formed a distinct regional group (50% bootstrap support). Populations sampled from the central coast and north coast regions of British Columbia did not cluster into distinct geographic units. Although some separation was observed, genetic differentiation between populations in the two regions was limited, and this was reflected in the lack of consistency in population clustering in the dendrograms evaluated.

Cluster analysis of the populations sampled in the even-year broodline revealed a general lack of consistency in geographically based clustering of the populations. The only exception was observed for the Skeena River drainage, where all seven populations sampled clustered together in 97% of dendrograms evaluated. There was some evidence for a weak association for 19 of 21 populations from the Queen Charlotte Islands, but the cluster was not well supported (22% bootstrap support). As with the odd-year broodline, populations sampled from the central coast and north coast regions of British Columbia did not cluster into distinct geographic units (Fig. 2), which again reflected the overall lack of genetic differentiation (F_{ST}=0.001) between populations in the two regions.

Discussion

In the current study of microsatellite variation in pink salmon, approximately 46,500 individuals were surveyed from 146 odd-year and 116 even-year populations, 16 microsatellites were analyzed encompassing 812 alleles, and 12–85 alleles were identified per locus. Sample size ranged from 18 to 755 individuals per population, with at least 100 individuals sampled in 127 of the 146 odd-year populations, and 92 of the 116 even-year populations. Only six odd-year and seven even-year populations had fewer than 40 individuals surveyed. With a range in the number of individuals sampled per population, sampling errors may have influenced the estimated allele frequencies within populations, particularly for populations with fewer than 40 individuals sampled. If sampling errors are large in estimation of allele frequencies, there is a potential for these errors to obscure genetic relationships among related populations. Kalinowski (2005) reported that loci with larger numbers of alleles produced estimates of genetic distance with lower coefficients of variation than loci with fewer numbers of alleles, without requiring larger sample sizes from each population. Given the results from the cluster analysis, variation in the number of individuals sampled per population likely did not result in misidentification of genetic relationships among populations.

Inferences from the genetic relationships of populations surveyed in our study were dependent upon accurate determination of population allele frequencies. Microsatellite alleles differ in size, but alleles of the same size at a locus in geographically separate populations may not have the same origin as a result of size homoplasy. Convergent mutations in different lineages may produce alleles of the same size, with the result that there may be greater differentiation among lineages than revealed by analysis of size variation alone. However, with over 800 alleles observed across all loci in the study, the large amount of variation present

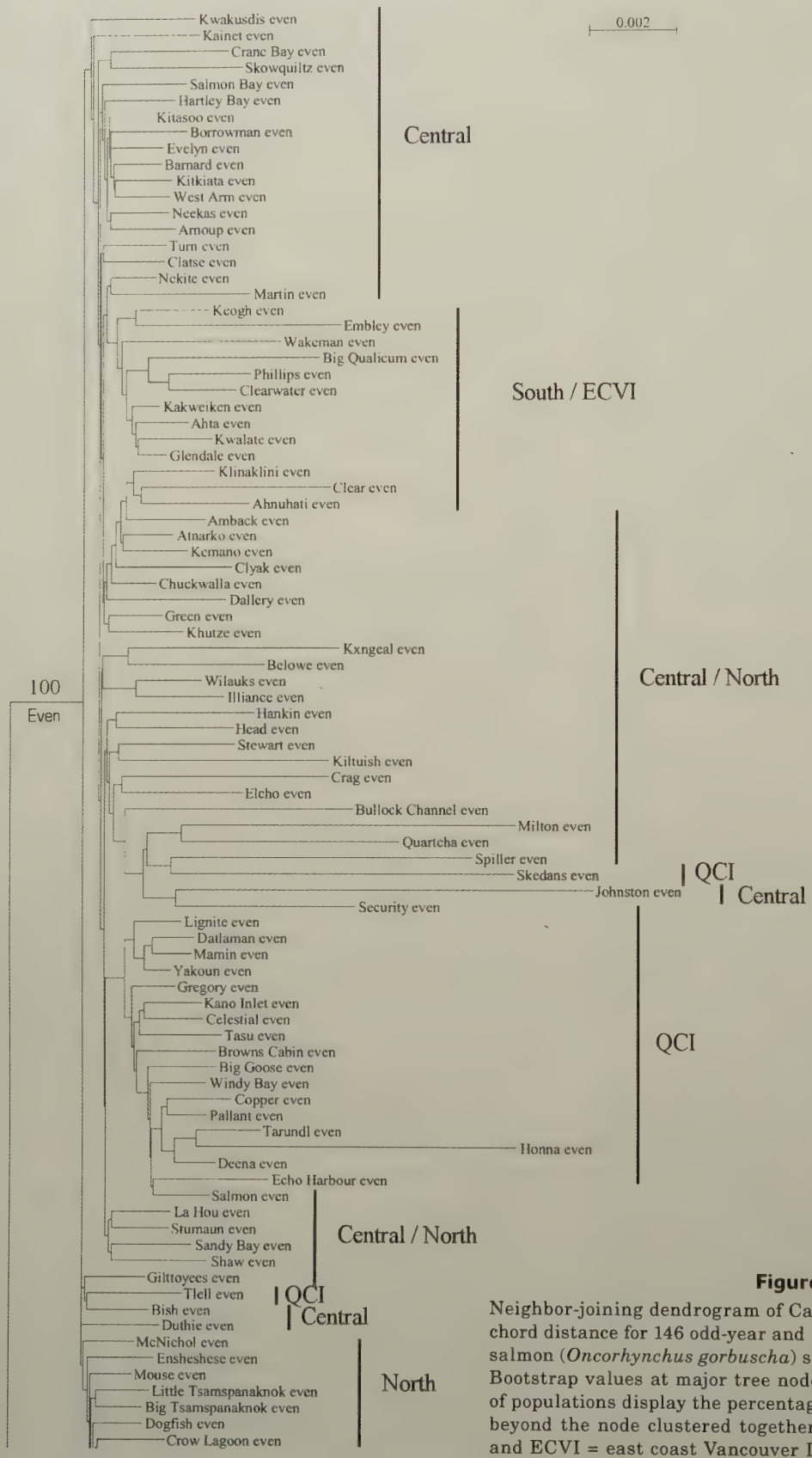

Figure 2

Neighbor-joining dendrogram of Cavalli-Sforza and Edwards (1967) chord distance for 146 odd-year and 116 even-year populations of pink salmon (*Oncorhynchus gorbuscha*) surveyed at 16 microsatellite loci. Bootstrap values at major tree nodes indicative of a regional group of populations display the percentage of 500 trees where populations beyond the node clustered together. QCI=Queen Charlotte Islands and ECVI = east coast Vancouver Island.

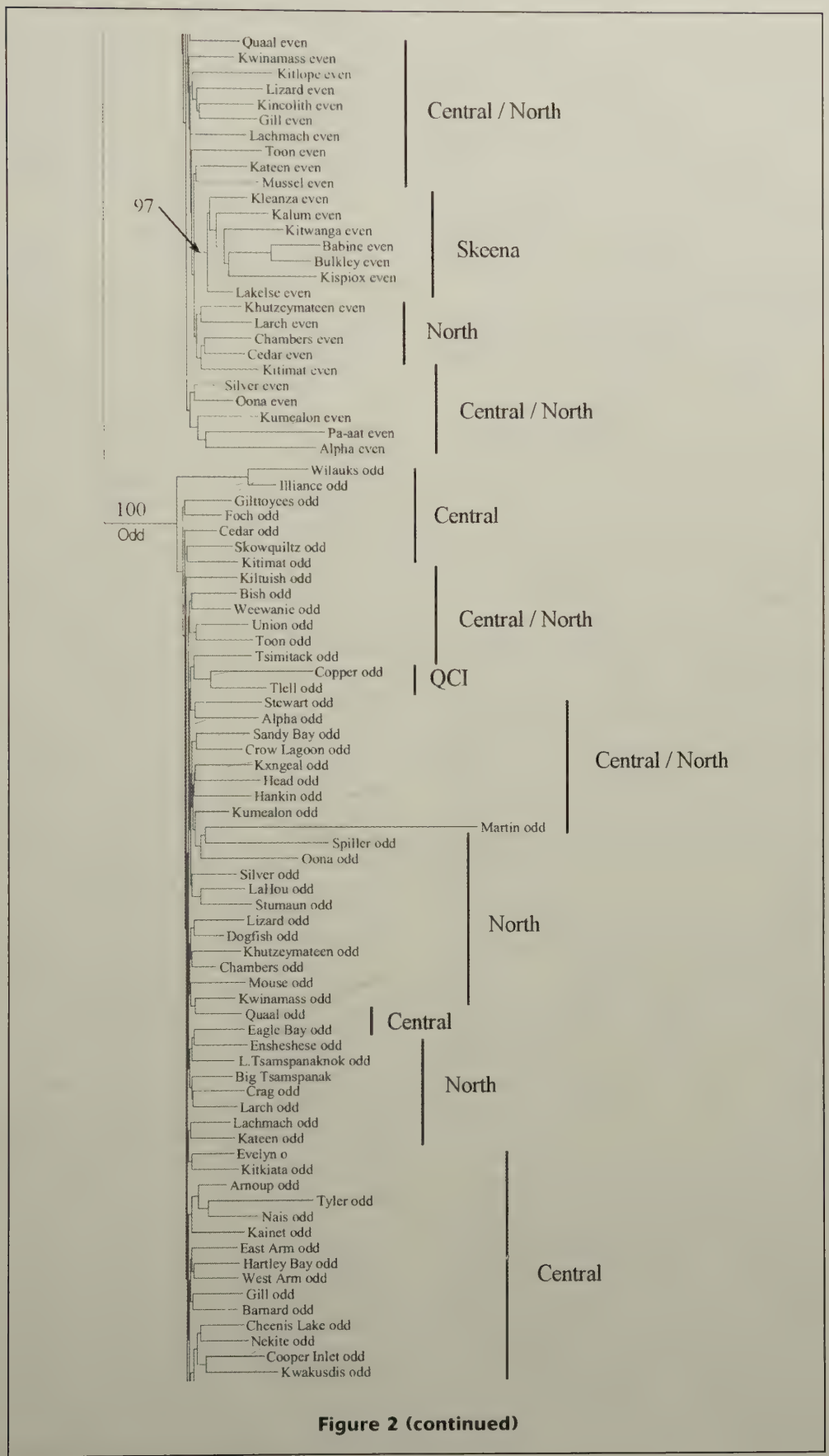

Figure 2 (continued)

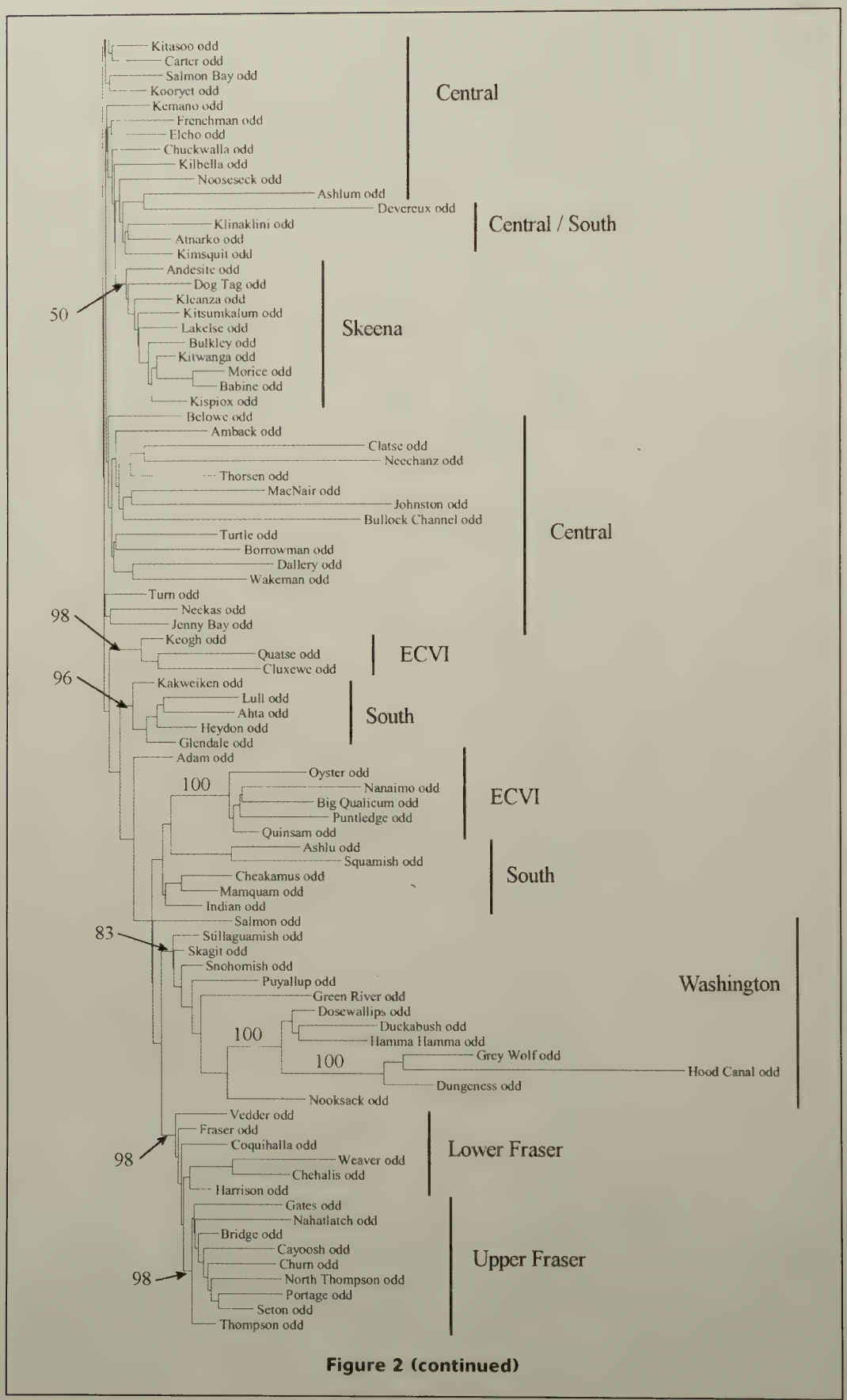

Figure 2 (continued)

at these loci largely compensates for size homoplasy (Estoup et al., 2002), and therefore the pattern of population structure identified was unlikely to be obscured or distorted by size homoplasy.

The distribution of genetic variance indicated that differences in allele frequencies between the broodlines were about three times greater than differences for all regional and population sources of variation, but that regional differences in allele frequencies were only about 1.4 times larger than differences among populations within regions. Previous analyses of annual variation in allele frequencies within populations have indicated that this source of variation can be as large as differences among populations within regions (Golovanov et al., 2009). Although not specifically illustrated in the current study because of limitations of the software to facilitate a four-level nested analysis of variance, similar results (not shown) were observed in the current study. The larger importance of annual variation within populations relative to population differentiation compared with other Pacific salmon species likely reflected the reduced population differentiation observed in pink salmon relative to that observed in other salmon species (Beacham et al., 2009, 2011).

The current study indicates that the largest determinant of population structure of pink salmon in British Columbia and Washington was year of spawning (odd or even), with a distinct separation of the two broodlines. With the odd-year broodline, regional differentiation was stronger in the southern portion of the distribution of populations, with the greatest population differentiation within a region observed in Washington. The Hood Canal hatchery population (also known as Hoodsport hatchery 47°23′37″N, 123°08′54″W) was the most distinct, even though this population was derived from adults returning to the Dungeness River and Dosewallips River in 1953 (Hard et al., 1996). The distinctiveness of this population was reflected in allelic frequency differentiation. For example, the frequency of the $One102^{311}$ allele was 0.54 in the Hood Canal hatchery population, 0.34 in the Gray Wolf River population, and <0.20 in all other Washington populations. Additionally, the frequency of $One109^{133}$ was 0.33 in the Hood Canal hatchery population, but <0.20 in all other Washington populations. All populations from drainages entering Hood Canal (Hood Canal hatchery, Dosewallips River, Duckabush River, Hamma Hamma River) or the Strait of Juan de Fuca (Dungeness River, Gray Wolf River) were distinct from those on the eastern side of Puget Sound (Snohomish River, Stillaguamish River, Skagit River, Green River, Puyallup River). Genetic separation of Strait of Juan de Fuca populations and Hood Canal populations from those in eastern Puget Sound was initially described by Shaklee et al. (1991) in an analysis of allozyme variation. However, as described by Shaklee et al. (1991), the Nooksack River population, located in the northeastern section of Puget Sound and nearest to the border with Canada, clustered with Hood Canal and Strait of Juan de Fuca populations, rather than with geographically closer populations on the east side of Puget Sound. Similar results were observed in the current study. Shaklee et al. (1991) suggested that the genetic similarity of the Nooksack River population to that of Hood Canal populations was a consequence of a 1977 transfer of fertilized eggs from the Hood Canal hatchery to a tributary of the Nooksack River and a reduction of the native population due to habitat degradation. As Shaklee et al. (1991) outlined, this enhancement effort may have caused a genetic change in the characteristics of this population that has persisted over time (Hard et al., 1996).

Fraser River populations were separate from those in southern British Columbia (east coast of Vancouver Island, south coast mainland) and Washington, confirming the results from the previous analysis of allozyme variation reported by Beacham et al. (1988) and Shaklee et al. (1991). In the Fraser River drainage, some separation was observed between populations spawning upstream from the Fraser River canyon (southern limit approximately 175 km upstream from the mouth) from those spawning downstream of the canyon. Genetic separation between upriver and downriver populations had also been had been outlined previously by Beacham et al. (1988) and Shaklee et al. (1991). Similar genetic separation between upper drainage and lower drainage populations has been observed in coho salmon (*O. kisutch*) (Beacham et al., 2011) and reflects geographic separation between the two groups of populations.

In northern British Columbia, odd-year broodline populations in the Skeena River drainage were separate from those farther south in the central coastal region of British Columbia and from those farther north on the northern coastal region of British Columbia in a similar pattern to that outlined by Beacham et al. (1988). Similar differentiation was also observed in the even-year broodline, with Skeena River drainage populations distinct from other populations in northern British Columbia. Some differentiation was observed in the current study between even-year broodline pink salmon populations from the Queen Charlotte Islands and other regions in northern British Columbia (central coast, Skeena River, north coast) (F_{ST} =0.004–0.006); differentiation of populations from the Queen Charlotte Islands had also been observed by Beacham et al. in 1988.

Studies of population structure in Pacific salmon are a useful initial step in developing and applying genetic variation to the problem of estimating stock composition in mixed-stock salmon fisheries. The key to successful application of genetic variation to estimation of stock composition centers around whether or not there is a regional basis to population structure. This is a key consideration because a regionally based population structure is generally required for genetic stock identification estimation, with the assumption that the portion of the mixed-stock sample derived from unsampled populations is allocated to sampled populations from the same region. With this assumption, the cost and complexity of developing a baseline for stock composition analysis is reduced, and refinements in estimated stock compositions are possible as the baseline is enhanced

in stages. For the odd-year broodline, applications in southern British Columbia would appear to be possible if fishery management objectives are to separate pink salmon of Washington, Fraser River, and southern British Columbia origin. Finer subdivision of stock composition estimation, particularly in the Washington region, may be possible, as separation of Hood Canal and Strait of Juan de Fuca populations from those in Puget Sound may be practical.

Studies of population structure in pink salmon have revealed some consistent patterns. The greatest differentiation observed in population structure has been consistently reported to occur between the two broodlines, whether in Asia or North America (Beacham et al., 1988; Kartavtsev, 1991; Varnavskaya and Beacham, 1992; Zhivotovsky et al., 1994; Salmenkova et al., 2006; Golovanov et al., 2009). In Asia, studies have indicated that genetic differentiation among populations is greater in the even-year broodline than in the odd-year broodline (Hawkins et al., 2002; Golovanov et al., 2009). In North America, the reverse situation occurs, with population differentiation among populations greater in the odd-year broodline than in the even-year broodline (Beacham et al., 1988; Gharrett et al., 1988; current study). These findings support the concept of two main refugia occupied by pink salmon during the most recent Pleistocene Era glaciation some 10,000 years ago (Aspinwall, 1974). The even-year broodline may have survived the glaciation in a northern refugium (Aspinwall, 1974). Once the glaciation ended, the even-year broodline dispersed from the northern refugium, colonizing southern regions more recently than northern ones. Conversely, the odd-year broodline may have occupied a southern refugium during the Pleistocene Era glaciation (McPhail and Lindsey, 1970), and dispersed northward, with northern populations derived more recently than southern ones. As populations closer to the refugium have had greater time to accumulate genetic mutations and thus display greater population differentiation, the current pattern of broodline and population differentiation is consistent with dispersal from a northern refugium for the even-year broodline (greater population genetic differentiation in even-year broodline) and dispersal from a southern origin for the odd-year broodline (greater population differentiation in odd-year broodline). Additionally, embryonic survival of the even-year broodline has been reported to be higher than that of the odd-year broodline in a cold (4°C) incubation environment, with higher alevin and fry growth of the even-year broodline also observed in the cold incubation environment (Beacham and Murray, 1988). Greater suitability of the even-year broodline to a colder environment is also illustrated by the spawning distributions of the broodlines in North America, with the even-year broodline in very low abundance from the southern portion of the range (Fraser River, Washington) and the odd-year broodline in low abundance in western Alaska. Alternatively, Krkošek al. (2011) suggested that the distribution of even-year and odd-year populations result from density-dependent mortality caused by interactions between the broodlines. However, it seems difficult to account for genetic population structure observed in pink salmon as a result of broodline interactions.

Conclusion

The level of differentiation observed among the pink salmon populations within broodlines surveyed in the current study was considerably less than in other species of Pacific salmon. Sockeye salmon (*O. nerka*) typically display high levels of genetic differentiation (F_{ST} =0.097, 14 loci, average 30 alleles per locus, 299 populations) (Beacham et al., 2006), with the other species displaying levels of genetic differentiation ranging between sockeye salmon and pink salmon. The low level of differentiation observed in pink salmon may be a result of a more recent colonization history (Hawkins et al., 2002), but may also be a result of straying among local populations within regions. As pink salmon juveniles spend little time in fresh water after fry emergence, imprinting on natal streams may not be as strong as in other species, and as a result may stray more upon returning spawning migrations (Quinn, 1993). Chum salmon (*O. keta*) juveniles spend similar amounts of time in fresh water as pink salmon, and population differentiation in the species is higher only than pink salmon (F_{ST} =0.033, 14 loci, average 57 alleles per locus, 380 populations) (Beacham et al., 2009). The low level of genetic differentiation observed in pink salmon population structure likely reflects higher levels of straying among populations during spawning than those observed for other Pacific salmon species.

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Evaluation of bioelectrical impedance analysis and Fulton's condition factor as nonlethal techniques for estimating short-term responses in postsmolt Atlantic salmon (*Salmo salar*) to food availability

Elaine M. Caldarone (contact author)[1]

Sharon A. MacLean[1]

Beth Sharack[2]

Email address for contact author: elaine.caldarone@noaa.gov

[1] Narragansett Laboratory
Northeast Fisheries Science Center
National Marine Fisheries Service
National Oceanic and Atmospheric Administration
28 Tarzwell Drive
Narragansett, Rhode Island 02882

[2] J. J. Howard Laboratory
Northeast Fisheries Science Center
National Marine Fisheries Service
National Oceanic and Atmospheric Administration
74 McGruder Road
Highlands, New Jersey 07732

Abstract—We evaluated measures of bioelectrical impedance analysis (BIA) and Fulton's condition factor (K) as potential nonlethal indices for detecting short-term changes in nutritional condition of postsmolt Atlantic salmon (*Salmo salar*). Fish reared in the laboratory for 27 days were fed, fasted, or fasted and then refed. Growth rates and proximate body composition (protein, fat, water) were measured in each fish to evaluate nutritional status and condition. Growth rates of fish responded rapidly to the absence or reintroduction of food, whereas body composition (% wet weight) remained relatively stable owing to isometric growth in fed fish and little loss of body constituents in fasted fish, resulting in nonsignificant differences in body composition among feeding treatments. The utility of BIA and Fulton's K as condition indices requires differences in body composition. In our study, BIA measures were not significantly different among the three feeding treatments, and only on the final day of sampling was K of fasted vs. fed fish significantly different. BIA measures were correlated with body composition content; however, wet weight was a better predictor of body composition on both a content and concentration (% wet weight) basis. Because fish were growing isometrically, neither BIA nor K was well correlated with growth rate. For immature fish, where growth rate, rather than energy reserves, is a more important indicator of fish condition, a nonlethal index that reflects short-term changes in growth rate or the potential for growth would be more suitable as a condition index than either BIA measures or Fulton's K.

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Populations of Atlantic salmon (*Salmo salar*) are broadly distributed across the North Atlantic Ocean, reproducing in coastal rivers of Iceland, Europe, northwestern Russia, and northeastern North America. Historically, native Atlantic salmon ranged throughout New England waters, but by the late 1880s, they were extirpated from many of the rivers. Currently, native populations exist only in central and southeast Maine (Northeast Fisheries Science Center, http://www.nefsc.noaa.gov/sos, accessed July 2011). A significant decline in these populations during the 1990s resulted in the listing of the Gulf of Maine Distinct Population Segment (DPS) as endangered under the United States Endangered Species Act (Federal Register, 2009). Hatchery-based restoration of salmon to this area began in 1970 and continues today. Although all life-stages have been released to the rivers, recent emphasis has focused on releasing fry and smolts produced in the hatchery from field-caught adults from the DPS region. Once smolts reach the sea, they must adapt to an environment and food source radically different from their freshwater habitats. To evaluate the success of these restoration efforts, managers need tools to assess whether hatchery-reared fish are thriving in the natural environment and to assess condition of the postsmolt Atlantic salmon population as a whole.

Growth rate and fat content are key measures of condition in fish. During a fish's early life-history stage, rapid growth rates increase the probability of survival and recruitment, primarily through decreased vulnerability to predation and starvation (see review by Fonseca and Cabral, 2007). Fat, the primary energy repository in marine fish, increases when food intake exceeds metabolic needs and decreases during food-limited times when it provides energy for maintenance, growth, and reproduction (Shulman and Love, 1999; Jobling, 2001). Growth rates of fish caught in the wild are often estimated by using nucleic acid analysis (the ratio of RNA to DNA) or otolith microstructure analysis (Chambers and Miller,

1995). The former requires removal of a plug of muscle tissue (MacLean et al., 2008), and the latter requires removal of an otolith, a lethal procedure. Direct measurement of fat content is also lethal, requiring chemical analysis of a sacrificed fish. Identifying a minimally invasive, nonlethal index that could estimate growth rate or body composition in postsmolt salmon would allow restoration managers to evaluate the condition of field-captured fish.

We chose to evaluate two nonlethal techniques which had the potential to reflect fish condition: bioelectrical impedance analysis (BIA) and Fulton's condition factor (hereafter, also called Fulton's K). BIA is a technique which has been applied to humans and other mammals as a means to estimate nutritional status and body composition (Baumgartner et al., 1988; Marchello and Slanger, 1994; Schwenk et al., 2000; Barbosa-Silva et al., 2003). Recently, BIA has been used to estimate body composition content in fish (Cox and Hartman, 2005; Pothoven et al., 2008; Hanson et al., 2010). For BIA, a small, portable, battery-operated instrument is used to generate a mild alternating current between two sets of electrodes that have been placed on the subject. The resulting voltage drop is recorded as resistance (R) and capacitive reactance (Xc) in series. When an alternating current passes around a cell, R can be affected by extracellular water (good conductor) and fat (poor conductor). When a constant signal frequency is applied, a geometrical system can be modeled as a cylinder (conductor volume = $\rho L^2/R$, where L is length) (Lukaski et al., 1985). With this conductor volume approach, predictive equations have been constructed to estimate water content and fat-free mass in humans (Lukaski et al., 1985; Chumlea et al., 2002), and water-, fat-, protein-, and ash-content in fish (Cox and Hartman, 2005; Pothoven et al., 2008; Hanson et al., 2010).

Impedance values have also been used to calculate a condition index (phase angle, arctangent Xc/R converted to degrees) in both humans and fish (Schwenk et al., 2000; Barbosa-Silva et al., 2003; Cox and Heintz, 2009). In an organism, Xc is a measure of the phase shift that results from an electrical charge being momentarily stored in the double phospholipid layer of a cell membrane. When cells die, Xc drops to zero; phase angles thus range from zero (zero Xc, all cells dead) to 90° (zero R). In humans, lower phase angle values have been associated with conditions such as reduced survival in HIV-infected patients, and malnutrition (Schwenk et al., 2000; Barbosa-Silva et al., 2003). In fish, significant decreases in phase angles have been observed in juvenile rainbow trout (*Oncorhynchus mykiss*) and brook trout (*Salvelinus fontinalis*) after three weeks of fasting, and in juvenile Chinook salmon (*O. tshawytscha*) after eight weeks of fasting (Cox and Heintz, 2009). In those studies, fish were repeatedly measured over a period of weeks with no mortalities associated with the BIA procedure—an attribute that made it attractive for our application.

Fulton's K (weight/length^3) (Ricker, 1975) is a widely used fish condition index based on morphometrics (e.g., Anderson and Gutreuter, 1983; Stevenson and Woods Jr., 2006), measurements that can be obtained easily in the field. This index is based on the assumption that within a cohort, individuals with higher K values (more rotund fish) contain more energy reserves (fat and protein), and thus are in better condition than those with lower K values.

The response time of a condition index can be affected by factors such as water temperature, life-stage, season, and species (Busacker et al., 1990). Cox and Heintz (2009) measured phase angles in food-deprived rainbow trout and brook trout on a weekly basis, and in food-deprived Chinook salmon intermittently for 13 weeks. Because our field recaptures of hatchery-reared postsmolts occur two to three weeks after release, we measured response of BIA measures and K to varying food availability every 3–4 days throughout a 3-week time period. Thus the objectives of our study were 1) to assess and validate the relations between two nonlethal condition indices (BIA measures and Fulton's condition factor) and two measures of nutritional condition (growth rate and body composition); and 2) to determine the short-term response time (days to a few weeks) of these measures to varying food availability.

Materials and methods

Smolts used in this study were progeny of field-caught Atlantic salmon from the Penobscot River, Maine, which had been spawned at Craig Brook National Fish Hatchery, East Orland, Maine, and reared at the Green Lake National Fish Hatchery, Ellsworth, Maine, for 13–15 months. Randomly selected smolts (52–113 g, 16–21 cm) were anesthetized in buffered tricaine methane sulfonate (MS-222, 150 mg/L) and implanted intramuscularly with a passive integrated transponder tag (PIT tag, Biomark, Boise, ID[1]) to permit identification of individuals. The smolts were then returned to the hatchery tank to allow time for full recovery, resumption of feeding, and removal of any tagging-related mortalities. Twenty-five days later the fish were transported to the University of Rhode Island's Blount Aquarium facility in Narragansett, Rhode Island, where they were randomly placed into two aerated, flow-through tanks (360-L capacity) initially filled with freshwater trucked from the hatchery. Over a period of five to six hours, freshwater was gradually replaced with sand-filtered seawater (10°C, 30 ppt). During the subsequent three weeks, while the fish were recovering from the transfer and acclimating to seawater, the water temperature was gradually raised to 12°C. During this period fish were fed to satiation twice per day with a commercial feed (Corey Optimum Hatchery Feed for Salmonids, Corey Nutrition Co., Fredericton, NB, Canada) supplemented with freeze-dried krill (*Euphausia pacifica*, Aquatic

[1] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 1

Sampling schedule for Atlantic salmon (*Salmo salar*) postsmolts reared at 12°C under three feeding regimens (fed; fasted; fasted then refed) in order to obtain a range of nutritional condition and growth rates. Nonlethal condition indices (Fulton's condition factor [*K*] and bioelectrical impedance analysis [BIA] measures) and two measures of nutritional condition (wet-weight based growth rate and proximate body composition) were determined for each fish. The refed group was fasted for 11 days and then fed. Numbers listed are number of fish sampled.

	Sampling day and feeding regimen											
	Day 0				Day 3			Day 7			Day 11		
	Base-line	Fed	Fasted	Refed	Fed	Fasted	Refed	Fed	Fasted	Refed	Fed	Fasted	Refed
Weight, length (Fulton's *K*)	5	24	24	22	4	4	0	4	4	0	4	4	22
BIA measures	5	24	24	0	4	4	0	4	4	0	4	4	0
Proximate body composition	5	0	0	0	4	4	0	4	4	0	4	4	0

	Sampling day and feeding regimen											
	Day 15			Day 19			Day 23			Day 27		
	Fed	Fasted	Refed	Fed	Fasted	Refed	Fed	Fasted	Refed	Fed	Fasted	Refed
Weight, length (Fulton's *K*)	4	4	5	4	4	5	4	4	5	0	0	7
BIA measures	4	4	5	4	4	5	4	4	5	0	0	7
Proximate body composition	4	4	5	4	4	5	4	4	5	0	0	7

Eco-Systems, Inc., Apopka, FL). Twenty-five days after the initial seawater transfer, when the now postsmolts appeared to be acclimated and feeding well, the experiment commenced (day 0).

Throughout the experiment, water temperature in each tank was recorded hourly with a HOBO® data logger (Onset Computer Corp., Bourne, MA), and ammonia levels and salinity were tested weekly. Water temperatures averaged 12.0°C, standard deviation (SD)=0.2; salinity averaged 31 ppt, SD=1; and the photoperiod was 15 hours of light to 9 hours of dark. Two-thirds of each tank surface was covered with black plastic to provide a low-light refuge, and the remaining third was exposed to overhead fluorescent lighting covered with red plastic. All experiments were conducted in accordance with guidelines established by the Institutional Animal Care and Use Committee (IACUC) at the University of Rhode Island.

Sampling protocols

Day 0 sampling On day 0, five fish were randomly selected and sacrificed to provide baseline body composition data. To obtain a range of nutritional condition levels, all remaining postsmolts were subdivided into three different feeding treatments (tanks): fed, fasted, and fasted then refed. The fed treatment (n=24) was continually fed, the fasted treatment (n=24) received no food, and the fasted, then refed treatment (n=22) received no food for 11 days followed by feeding for 16 days. Individuals were anesthetized with buffered MS-222 (150 mg/L) in chilled (12°C) seawater, blotted dry, measured for initial weight (wet weight, *WW*, nearest 0.1 g) and fork length (FL, nearest 0.1 cm), and the PIT tag number and any gross external abnormalities were noted. BIA measurements were taken on all fish assigned to the fed and fasted treatments. Fish assigned to the fasted, then refed treatment had their fork length and wet weight recorded at the start of their fasting (day 0), and again on day 11 when they were fed for the remainder of the experiment. Total handling time per fish for wet weight, fork length, and BIA measurements was no more than 30 seconds.

During daylight hours, fish in the fed treatment and refed group were provided freeze-dried krill *ad libitum* from a belt feeder. On days fish were sampled, no food was provided until after sampling was completed (~1200).

Days 3–27 sampling In order to determine the response time of BIA measures and *K* to the three feeding treatments, and to construct predictive equations for body composition, fish were sampled and sacrificed every three to four days over a 23–27 day period. On day 3 and every 4 days thereafter, 4 fish each from the fed and fasted treatments were sacrificed. On day 15 and every 4 days thereafter, 5 fish from the refed group were sacrificed and sampled, except on the final day when 7 fish were sacrificed (Table 1).

All fish were killed by an overdose of buffered MS-222 (300 mg/L) in chilled (12°C) seawater. The fish were immediately blotted dry, measurements of wet weight, fork length, and BIA (in that order) were taken, and PIT tag numbers and external abnormalities were noted. Internal temperatures (muscle and stomach) were determined by inserting an instant-read digital thermometer into the dorsal musculature of the fish, and down the esophagus into the stomach. Total sampling time for each fish was ~1.5 min. Each fish was then dissected, its liver removed, its gut evacuated, and sex and maturity status was determined. Livers and carcasses were wrapped separately in aluminum foil before being vacuum-sealed in plastic bags and stored frozen at −80°C until subsequent analysis.

Body composition analysis Liver and carcass wet weights were determined to the nearest 0.1 mg before being freeze-dried to a constant weight and reweighed. Each dried sample was ground in a Foss Tecator® Cyclotec 1093 sample mill (FOSS, Hilerød, Denmark) and stored at −20°C in glass scintillation vials under nitrogen gas until further analysis. Total water (*TWa*) was calculated by subtracting total dry weight (liver dry weight plus carcass dry weight, *DW*) from total wet weight.

Freeze-dried carcasses were analyzed for proximate body composition (protein, fat, ash) by an independent laboratory (A&L Great Lakes Laboratory, Fort Wayne, IN) by using Association of Official Analytical Chemists international certified methods and were reported to us on a percent DW basis. Nitrogen was determined by using a LECO nitrogen combustion analyzer (LECO Corp., St. Joseph, MI; Dumas method), protein was calculated by multiplying nitrogen values by 6.25 (Jones, 1931), fat was obtained with a 4-hr ether reflux extraction, and ash was determined after combustion at 600°C for 2–4 hr. Body composition (g) (total amount of each proximate body constituent) were calculated from percent dry weight concentrations by dividing the independent laboratory values by 100 and multiplying by the total dry weight. To conform to the format most often reported in the literature, percent dry-weight-based concentrations were converted to a percent wet-weight-based concentration by dividing body composition (g) by wet weight and multiplying by 100 (body composition [%WW]).

Liver lipids, which are often mobilized first during fasting (Love, 1970; Black and Love, 1986), were measured separately in order to detect changes more easily. Liver lipid content was determined in-house by using a modification of Folch et al. (1957). Entire freeze-dried livers were first extracted by ultrasonic homogenization with 2:1 methylene chloride:methanol solvent (20 mL/g tissue), then back extracted with aqueous 0.1 M KCl and centrifuged to remove water, methanol, and water-soluble and water-insoluble tissue components by phase separation. The remaining nonaqueous fractions were evaporated to remove methylene chloride, and the nonvolatile lipid residue was weighed on a Mettler® AE240 balance (nearest mg, Mettler-Toledo, Inc., Columbus, OH). Individual livers were not analyzed for protein or ash because of their small size; therefore body composition values were obtained for carcass water, liver water, total water (liver water plus carcass water), carcass fat, liver fat, total fat (liver fat plus carcass fat), carcass protein, and carcass ash.

Growth-rate calculations

Individual instantaneous wet-weight based growth rates were calculated with the following formula (Ricker, 1979):

$$\textit{growth rate}\ (\text{per d}) = (\ln WW_{t2} - \ln WW_{t1})/(t_2 - t_1)\ , \quad (1)$$

where WW = the wet weight of an individual at time t (day).

Growth rates for fish in the fed and fasted treatments were calculated from day 0 (t_1) until the day they were sacrificed (t_2). For the fasted portion of the fasted, then refed treatment, growth rates were calculated from day 0 (t_1) until day 11 (t_2); for the refed portion, growth rates were calculated from the first day of refeeding (day 11, t_1) until the day they were sacrificed (t_2). Growth rates calculated over intervals of less than five days were excluded from our analyses because minimal weight changes over those short time intervals, combined with the inherent variability of measuring wet weight, resulted in inaccurate growth rate estimates.

BIA measurement protocol and BIA measures

BIA measurements were determined with a Quantum-X® (RJL Systems, Point Heron, MI) four-electrode single frequency (800 μA, 50 KHz) analyzer. Needle electrode probes were constructed in-house according to Cox and Hartman (2005). For each probe, two 12-mm×28-gauge electroencephalographic (EEG) needles (Grass Telefactor, West Warwick, RI) were mounted in balsam wood 1 cm apart and with 0.5 cm of the needle exposed. The fish were placed on their right sides on a nonconductive board. The detector electrode of the anterior probe was inserted midway between the posterior edge of the operculum and the leading edge of the dorsal fin, and midway between the base of the dorsal fin and the lateral line. The signal electrode of the posterior probe was inserted at the leading edge of the adipose fin, and midway between the base of the adipose fin and the lateral line. Serial *R*, serial *Xc*, and the distance between the inside (detector) electrodes, were recorded for each fish.

All BIA measures were initially calculated by using both their series and parallel forms. Results of statistical analyses indicated that the parallel forms were more highly correlated to the independent variables. For this reason, as well as the instrument manufacturer's recommendation that the parallel forms most

closely approximate the real electrical values of biological tissue (RJL Systems, http://www.rjlsystems.com/docs/bia_info/principles/, accessed April 2008), only the parallel forms of the BIA measures are discussed and reported.

Serial R and Xc values were transformed to their parallel equivalents with the following formulas:

$$R_{par}(\Omega) = R + Xc^2/R, \quad (2)$$

$$Xc_{par}(\Omega) = Xc + R^2/Xc\,. \quad (3)$$

Because R and Xc are dependent upon the distance the current must travel (D, distance between the electrodes in cm), the BIA instrument manufacturer advises that when these variables are used in prediction equations, the effect of this distance must be accounted for (RJL Systems, http://www.rjlsystems.com/docs/bia_info/principles/, accessed April 2008). We therefore also calculated standardized R_{par} and Xc_{par} values by dividing R_{par} and Xc_{par} by D (R_{par}/D, Xc_{par}/D).

Conductor volumes were calculated by using the following formulas:

$$R_{par}\ conductor\ volume = D^2/R_{par}\,, \quad (4)$$

$$Xc_{par}\ conductor\ volume = D^2/Xc_{par}\,. \quad (5)$$

Capacitance (a measure of the electrical storage capacity) and impedance (a measure of the opposition to the flow of electrical current) were calculated using the following formulas:

$$capacitance\ (\mathrm{pF}) = 1 \times 10^{12}/(2\pi \bullet 50000 \bullet Xc_{par}), \quad (6)$$

$$impedance\ (\Omega) = \mathrm{sqrt}((R_{par}^2) + (Xc_{par}^2))\,, \quad (7)$$

where 50,000 is the frequency applied by the BIA instrument in Hertz.

In order to conform to values previously reported in the literature, phase angles were calculated with Xc and R in their series form:

$$phase\ angle\ (^\circ) = \arctan(Xc/R) \bullet 180/\pi, \quad (8)$$

where Xc and R are the vertical and horizontal axis, respectively. The arctangent of the ratio will yield the angle of the impedance vector in radians, which is then converted to degrees by multiplying by $180/\pi$. A series-based phase angle is equal to 90° minus the parallel-based phase angle.

Impedance measurements are negatively related to temperature (van Marken Lichtenbelt, 2001). Water temperature, room temperature, and internal fish temperatures (mean muscle temperature=13.4°C, SD=0.9; mean stomach temperature=12.6°C, SD=1.0) were constant in our study and therefore not included as factors in our analyses. Unless otherwise noted, the term "BIA measures" refers collectively to R_{par}, Xc_{par}, R_{par}/D, Xc_{par}/D, *phase angle*, R_{par} and Xc_{par} *conductor volumes*, *capacitance*, and *impedance*.

Fulton's *K*

Fulton's condition factor (K) was calculated with the following formula (Ricker, 1975):

$$K = 100 \bullet WW/FL^3\,, \quad (9)$$

where WW (in g) and FL (in cm) are values from the day the fish was sacrificed.

Data analysis

Within treatments A Dunnett two-tailed t-test with final FL as a covariate was used to detect changes in body composition (% WW), BIA measures, and K, within the fed and fasted treatments and the refed group. Baseline values (day 0) were specified as the control for all variables except BIA measures, where day-3 fed values were the specified controls.

Between treatments A two-way multivariate analysis of covariance (MANCOVA) for unbalanced design was used to compare body composition (%WW) (total fat concentration, $TF\%$; total water concentration, $TWa\%$; carcass protein concentration, $CP\%$), BIA measures, growth rate, and K between the three feeding treatments (fed; fasted; fasted, then refed) and sampling times, with final FL as the covariate. When interactions were significant, feeding treatment was nested in day and follow-up comparisons were examined by using Tukey's HSD multiple range tests. Because we found no significant differences in percent liver fat between any of the treatments or days, and liver fats comprised <1% of total fats (range: 0.39–0.99%), only total fat values were used in all analyses.

Prediction models Prediction models for body composition expressed as both content (total fat, TF; TWa; carcass protein, CP), and concentration ($CP\%$, $TF\%$, $TWa\%$), and growth rate were developed. We used an information-theoretic approach for small sample sizes (Akaike's information criterion, AICc) to select the "best-fit" models (Wagenmakers and Farrell, 2004). Because we had no prior knowledge of the variables or combination of variables that would be the best predictors of the dependent variables, all nine BIA measures plus the interaction of R_{par}, and Xc_{par} with D were tested, along with WW, FL, and K. Testing 14 independent variables generated a large number of models for each dependent variable, with many models significant at the $P<0.0001$ level. For brevity, only the top three most parsimonious models (as indicated by the smallest AICc values) are reported and discussed.

Correlations Pearson product-moment correlations were used to investigate the relations between body composition (both g and %WW), and WW, BIA measures, K, and growth rate. All statistical analyses were carried out with SAS software vers. 9.1 (SAS Inst., Inc., Cary,

Table 2

Proximate body composition (% whole-body wet weight), capacitance, and % change in wet weight of Atlantic salmon (*Salmo salar*) postsmolts reared at 12°C under 3 feeding regimens (fed; fasted; fasted then refed). The refed group was fasted for 11 days and then fed. *TF%*=total fat concentration; *TWa%*=total water concentration; *CP%*=carcass protein concentration. *Capacitance* (pF) is a measure of the electrical storage capacity of cells. Percent change in wet weight was calculated by subtracting the initial wet weight of a fish on day 0 (fed and fasted treatments) or day 11 (fasted then refed treatment, day they were fed) from its wet weight on the day it was sacrificed, expressed as a percent of its initial wet weight. Asterisks (*) in the body composition columns indicate a significant difference from baseline values, and in the capacitance column they indicate a significant difference from day 3 fed values (Dunnett two-tailed *t*-test, $P \leq 0.05$). Values are means with standard deviation (SD) in parentheses. Mean initial wet weight of all fish was 76.0 g (SD=12.6, [no. of fish sampled=74]). NA=not available. *n*=number of fish sampled.

Feeding regimen	Sampling day	*n*	*TF%*	*TWa%*	*CP%*	*Capacitance*	% change in wet weight
Baseline	0	5	7.1 (1.1)	73.2 (1.2)	17.6 (0.5)	NA	0
Fed	3	4	7.4 (1.8)	73.9 (1.5)	17.0 (0.4)	2275 (322)	NA
	7	4	6.3 (1.4)	74.1 (1.3)	17.4 (0.7)	2057 (66)	1.2 (1.9)
	11	4	5.9 (0.9)	74.9 (1.3)	16.9 (0.7)	2012 (333)	9.0 (2.3)
	15	4	5.5 (0.8)	74.9 (1.0)	17.4 (0.4)	2144 (150)	15.5 (6.5)
	19	4	6.2 (1.1)	73.8 (1.3)	17.8 (0.3)	2024 (113)	25.9 (5.0)
	23	4	6.7 (2.0)	73.9 (2.6)	17.6 (0.7)	2024 (126)	20.7 (7.2)
Fasted	3	4	7.9 (1.2)	72.6 (1.1)	17.0 (1.0)	2112 (268)	NA
	7	4	6.4 (1.3)	74.8 (1.6)	16.6 (0.4)	2042 (156)	−2.7 (0.8)
	11	4	6.0 (1.0)	74.5 (1.2)	16.9 (0.2)	1861 (180)*	−4.2 (0.9)
	15	4	5.2 (0.6)*	75.9 (1.1)*	17.0 (1.0)	1919 (152)*	−4.6 (1.4)
	19	3	5.3 (1.6)	75.8 (1.6)*	17.3 (0.2)	1988 (175)	−7.3 (2.5)
	23	4	4.9 (1.1)*	76.5 (1.5)*	16.2 (1.1)	1744 (297)*	−7.3 (2.5)
Fasted, then refed	15	5	6.5 (2.1)	74.8 (2.8)	17.3 (0.9)	2005 (228)	NA
	19	5	5.7 (0.8)	75.7 (1.2)	16.8 (0.7)	1876 (151)	4.0 (4.5)
	23	5	5.8 (0.8)	74.7 (0.9)	17.4 (0.7)	1978 (136)	17.5 (2.7)
	27	7	5.8 (0.8)	75.1 (0.7)	17.2 (0.5)	1953 (74)	15.5 (5.9)

NC). Unless otherwise stated, the level of significance was set at $P \leq 0.05$.

Results

General observations

At the start of the experiment we observed frayed or eroded dorsal fins in ~78% of the fish, and fraying of the pelvic fin in ~12% of the fish. During the experiment there was no change in the frequency of these abnormalities and there were no mortalities; however, one severely emaciated, moribund fish was excluded from the data set. None of the fish had well developed gonads and therefore all were considered to be immature. Because sex did not emerge as a significant factor in any of the statistical analyses, it was not included in the data set.

Within two weeks after their transfer to seawater, the postsmolts were actively feeding and appeared to be acclimated to the seawater and their surroundings. On day 0, wet weight ranged from 43 to 132 g, and fork length from 18 to 23 cm; size distributions of fish were not significantly different between feeding treatments (fed mean=76 g, SD=12; fasted mean=75 g, SD=13; fasted then refed mean=80 g, SD=4).

On day 0 we encountered instability problems with our handmade probes, which were resolved by the end of the day. Because we were not completely confident in our BIA measurements that day, we have not included these initial BIA values in any of our analyses. Currently, BIA needle-electrodes are not manufactured and must be made in-house. Standardized manufactured probes would be necessary if BIA is to be routinely used.

Within-treatment effects

Over the course of the experiment, changes in fish weight and body composition (%WW) were observed within a treatment. On the final day of the experiment, fish in the fed treatment had increased in weight by 14–28%, whereas fasted fish had lost 5–10% of their weight (Table 2). Fish in the fasted, then refed treatment lost an average of 4% in weight during their 11 days without food, and gained 10–21% after 16 days of refeeding. Within each of the 3 feeding treatments, *CP%* (Table 2) and *CA%* (not shown) remained fairly constant. Changes in *TF%* (decreasing) and *TWa%* (increasing) occurred in fasted fish only, and differences from baseline values became significant after 15 d of fasting (Table 2). Within a treatment and sampling day, *TF%* was the most variable of the body components, averaging an

18% coefficient of variation (CV) compared to 3.7% for *CP%* and 1.9% for *TWa%*. In continually fasted fish only, changes in two BIA measures from day-3 fed values were observed: capacitance significantly decreased beginning on day 11 (Table 2) and impedance increased on day 23 only (not shown).

Between-treatment effects

Results of the MANCOVA indicated that of the variables tested (body composition [%WW], BIA measures, growth rate, *K*), only growth rate ($P<0.0001$, df=13) and *K* ($P=0.0009$, df=16) revealed significant differences due to feeding treatment. Results of Tukey's HSD multiple range tests indicated that beginning on day 11 and continuing until the end of the experiment, growth rates (negative) of the continually fasted fish were statistically significantly slower than the fed treatment (Fig. 1A). Eight days after refeeding (day 19), growth rates of the refed group were significantly faster than those of the continually fasted treatment. On day 19 the fed treatment also had faster growth rates than those of the refed group, whereas the relation was reversed on day 23. On day 23, *K* values were significantly smaller in the continually fasted fish than those of the fed fish (Fig. 1B). There was a trend of higher mean phase angle values in the fed treatment than those in the fasted treatment (Fig. 1C), but the values between the feeding treatments were not statistically different owing to high variability within a day's sample.

Prediction models

Body composition (g), R_{par}, and Xc_{par} measured in the postsmolts encompassed a range of values (Table 3). The best predictor models for body composition (g) all contained *WW* and *FL* as independent variables, with some models also including BIA measures or *K* (Table 4). In these models, *K* can be viewed as an interaction term between *WW* and *FL* (i.e., a size-related variable). The models for *TWa* and *CP* had high predictive capabilities (coefficient of determination (r^2)>0.98),whereas the model for *TF* was less so (r^2 range: 0.74–0.76). Adding any of the BIA measures to models containing only size or size-related independent variables (size-based-only models) increased the explanatory capabilities by <1.5%.

The best predictor models for body composition (%WW) also contained size-related variables (*WW* or *FL*, and often *K*) (Table 4). The models for *CP%* additionally contained two or three BIA measures. Adding the BIA measures to a size-based-only *CP%* model increased the explanatory capabilities by <3.4%.

The best predictor models for growth rate included size-related variables plus two BIA measures (Table 4). Adding the two BIA measures to size-based-only models increased the predictive capability of the growth equations by 18–22%.

Models with ΔAICc values ≤2 are considered to be equally probable to the "best fit" model (Burnham and Anderson, 2002). Based on the ΔAICc and r^2 values,

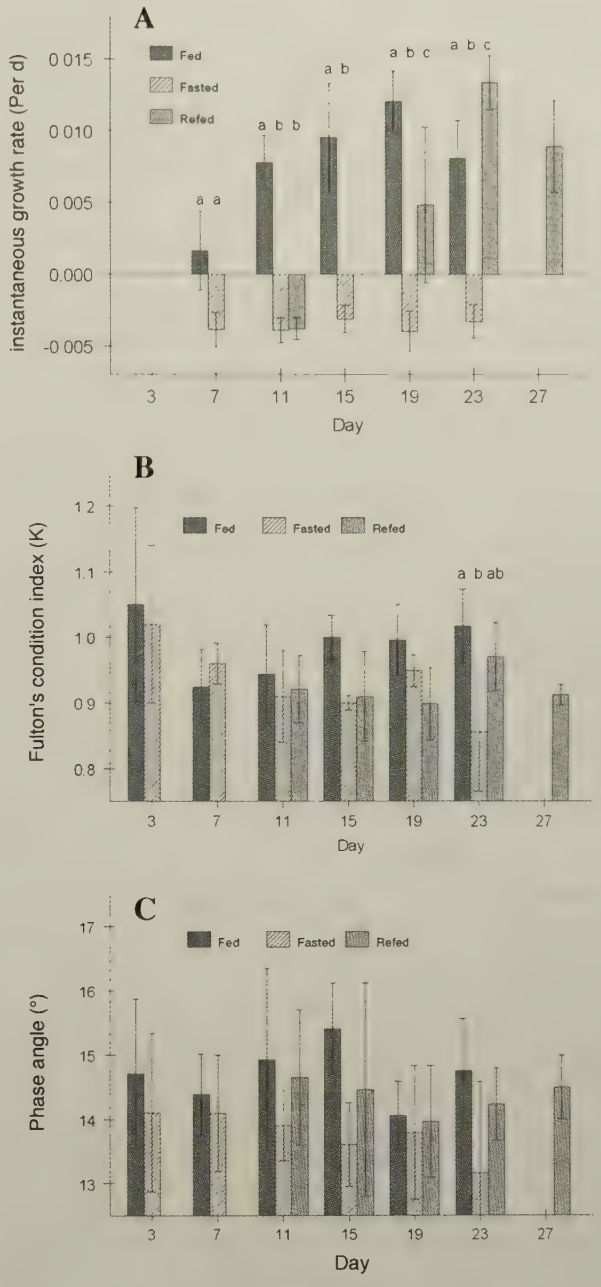

Figure 1

(**A**) Instantaneous wet-weight-based growth rate (per d); (**B**) Fulton's condition factor (K= 100•final wet weight/fork length^3); and (**C**) phase angle (arctangent reactance/resistance converted to degrees) of laboratory-reared Atlantic salmon (*Salmo salar*) postsmolts measured over 27 days. Values are mean (±standard deviation [SD]) for each sampling day. Fish were either fed *ad libitum*, fasted, or fasted until day 11 and then fed for the remainder of the experiment (refed). Within a sampling day, food treatments sharing a common superscript or without superscripts do not differ significantly (Tukey's HSD multiple range tests). For fed and fasted fish n=4 for each sampling day. For refed fish n=22 for day 11, n=5 for days 15, 19, and 23, and n=7 for day 27.

little difference was evident between the top three models for each dependent variable measured. Statistical significance of all models was high ($P<0.0001$); however, the predictive capability of the body composition content (g) models (74–99%) was much higher than the concentration (%WW) and growth rate models (all <50%), with the *TF%* models having the lowest explanatory capability (<33%).

Correlations

Body composition (g) values were most highly correlated with *WW* (Table 5), although *CP* and *TWa* were also well correlated with Xc_{par} *conductor volume* (Table 5). *CP* and *TWa* were highly positively correlated with each other, and *TF* and *TWa* were less so; thus the majority of the changes in *WW* would be from the relation of water to protein, not water to fat. The ratio of water to protein averaged 4.4 (SD=0.2), which is very similar to the value reported by Breck (2008) from other studies.

Variables most highly correlated with *TF%* (positively) and *TWa%* (negatively) were *WW* and *K* (Table 5), whereas *CP%* and growth rate were most correlated with *WW*. *TF%*, *TWa%*, and *CP%* had no or low correlation with growth rate, indicating that the fish were growing isometrically and not storing fat (Table 5). Overall, correlations of body composition (%WW) were much lower than correlations of body composition (g) with *WW*, BIA measures, and *K*.

Discussion

Treatment effects

Feeding treatment (fed; fasted; fasted then refed) clearly impacted weight-based growth rates of postsmolt salmon. Growth rates of fed fish (mean=0.0078/d; range: −0.0018 to 0.0139/d) were significantly faster than those of fasted fish (mean=−0.0036/d; range: −0.0020 to −0.0053/d) and fell within ranges reported for other laboratory studies using similarly aged Atlantic salmon postsmolts (Handeland et al., 2000; Jobling et al., 2002; Bendiksen et al., 2003; Sissener et al., 2009). Growth rates of fish responded quickly to the absence or reintroduction of food; decreasing after seven days of fasting, and increasing eight days after refeeding. Wilkinson et al. (2006) reported a similar response time for growth rates of Atlantic salmon smolts after 15 days of fasting (their first sampling date) and seven days of refeeding. Somatic growth rate in immature fish is an important index of condition because faster growers are considered to have a higher probability of survival (Lundvall et al., 1999; Craig et al., 2006; Fonseca and Cabral, 2007). Rapid growth rate, which results in larger individuals, is also thought to be critical for over-winter survival (Beamish and Mahnken, 2001). The widespread importance of rapid growth rates during early life history stages is demonstrated in a meta-analysis of 40 fish studies (Perez and Munch, 2010) where 77% of estimated selection differentials favored a larger fish size during this stage.

Table 3

Mean, standard deviation (SD) in parentheses, and range of body composition (g) and bioelectrical impedance analysis measures (BIA; parallel resistance [R_{par}] and reactance [Xc_{par}]) of postsmolt salmon (*Salmo salar*) reared at 12°C and three feeding regimens in order to obtain a range of nutritional condition. Fish weight ranged from 43 to 132g and length from 18 to 23 cm (no. of fish sampled=74).

Variable	Mean	Range
Total water content (*TWa*) (g)	60.0 (11)	33.7–92.4
Carcass protein content (*CP*) (g)	13.7 (3.1)	6.4–24.3
Total fat content (*TF*) (g)	5.1 (1.8)	1.8–12.7
Carcass ash content (*CA*) (g)	1.9 (0.4)	1.0–3.0
R_{par} (Ω)	408 (24)	340–480
Xc_{par} (Ω)	1613 (178)	1204–2437

During our study there was little impact of feeding treatment on the body composition (%WW) of postsmolt salmon. The reason for this relative constancy among feeding treatments was two-fold: 1) isometric growth in fed fish resulted in stable body composition (%WW) throughout a range of growth rates; and 2) there was little loss of proximate body constituents in fasting fish. When excess energy in young fish is directed primarily toward isometric growth, differences in growth rate cannot be discerned from body composition (%WW). For this reason, indices based on body composition (%WW) may not be the best metrics for assigning nutritional status and condition in immature fish.

Generally, fish are well adapted to fluctuations in the food supply—a scenario they encounter often in the wild (Jobling, 2001). Atlantic salmon and other fish can respond to instances of food deprivation by reducing oxygen consumption, resulting in a decreased rate of fat and protein catabolism (Beamish, 1964; Metcalfe, 1998; O'Connor et al., 2000). Our results indicate that fasted postsmolts used only a small portion of fat for their metabolic needs during the 3-week experiment. The combination of isometric growth in the fed fish, and short-term food deprivation period in the fasting fish, resulted in nonsignificant differences in body composition (%WW) among the feeding treatments.

The utility of BIA as a condition index is based on differences in proportions of body constituents translating into measurable differences in impedance when an electric current is applied. Because body composition (%WW) of the postsmolts did not differ among the feeding treatments, it was not surprising that none of the nine BIA measures differed among the feeding treatments. Within the fasted treatment, capacitance values did decrease with increasing time fasted, possibly reflecting the decline in fat concentration in this

Table 4

Coefficients and Akaike's second-order information criterion for small sample sizes (AIC_c) for the top 3 most parsimonious regression models for proximate body composition (expressed as g and % wet weight) and growth rate of postsmolt Atlantic salmon (*Salmo salar*) reared at 12°C under 3 feeding regimens in order to obtain a range of nutritional condition and growth rates. *WW*=wet weight (g); *FL*=fork length (cm); R_{par}=resistance in parallel (Ω); Xc_{par}=reactance in parallel (Ω); *D*=distance between bioelectric impedance detector electrodes (cm); R_{par} *conductor volume*=D^2/R_{par}; *K*=Fulton's K ($100 \cdot WW/FL^3$); *capacitance* (pF) is a measure of the electrical storage capacity of cells; *impedance* (Ω) is a measure of the opposition to the flow of electrical current; R_{par}/D=R_{par} standardized for *D*; *phase angle* (°)=arctangent of Xc/R converted to degrees; Δ*AICc*=difference in *AICc* values with respect to the most parsimonious model. For all models $P<0.0001$. r^2 = coefficient of determination.

Dependent variable	*n*	Model	r^2	AICc	ΔAICc
Total fat content (*TF*)(g)	60	$0.733 + 0.172(WW) - 0.696(FL) + 0.090(R_{par}/D)$	0.755	−6.72	0
		$8.326 + 0.150(WW) - 0.755(FL)$	0.742	−5.71	1.0
		$6.573 + 0.173(WW) - 0.648(FL) - 54.90(R_{par}\ conductor\ volume)$	0.750	−5.49	1.2
Carcass protein content (*CP*)(g)	65	$13.794 + 0.260(WW) - 0.825(FL) - 4.453(K)$	0.985	−119.18	0
		$28.269 + 0.285(WW) - 1.131(FL) - 0.002(capacitance) - 0.002(impedance) - 6.62(K)$	0.986	−117.97	1.2
		$2.261 + 0.215(WW) - 0.234(FL) - 0.0005(capacitance)$	0.985	−117.16	2.0
Total water content (*TWa*)(g)	67	$-12.187 + 0.616(WW) + 1.109(FL)$	0.993	−3.20	0
		$-30.19 + 0.541(WW) + 2.002(FL) + 6.210(K)$	0.993	−2.93	0.3
		$-7.791 + 603(WW) + 1.087(FL) - 0.055(R_{par}/D)$	0.993	−2.35	0.8
Total fat concentration (*TF*%)	60	$15.272 + 0.099(WW) - 0.842(FL)$	0.326	9.81	0
		$-1.568 + 0.28(WW) + 5.70(K)$	0.324	10.02	0.2
		$8.086 + 0.330(FL) + 7.910(K)$	0.318	10.55	0.7
Carcass protein concentration (*CP*%)	65	$32.185 + 0.044(WW) - 0.218(FL) - 0.004(capacitance) - 0.004(impedance)$	0.503	−83.17	0
		$27.318 + 0.026(WW) - 0.003(capacitance) - 0.004(impedance)$	0.483	−82.96	0.2
		$28.090 + 0.036(WW) + 0.041(R_{par}/D) - 0.004(capacitance) - 0.005(impedance)$	0.498	−82.52	0.6
Total water concentration (*TWa*%)	67	$86.901 - 0.044(WW) - 9.180(K)$	0.499	20.00	0
		$97.183 - 0.522(FL) - 12.553(K)$	0.496	20.35	0.3
		$60.435 - 0.154(WW) - 1.310(FL)$	0.485	21.86	1.9
Instantaneous wet-weight based growth rate (per day)	56	$-0.6866 - 0.0016(WW) + 0.0219(FL) + 0.3882(R_{par}\ conductor\ volume) + 0.0025(R_{par}/D) + 0.1931(K)$	0.481	−582.29	0
		$-0.1087 + 0.0033(FL) - 0.00003(capacitance) + 0.00374(phase\ angle) + 0.0560(K)$	0.453	−581.85	0.4
		$-0.2156 + 0.0034(FL) + 0.00003(impedance) + 0.0031(phase\ angle) + 0.0578(K)$	0.444	−580.98	1.3

group. However, when the whole data set was examined, capacitance and fat concentration (range: 4–10%) were only somewhat correlated (coefficient of correlation [*r*]=0.41, $P<0.005$).

Isometric growth is assumed for Fulton's *K*, and differences in the weight–length relation are interpreted as an indication of stored energy. Because the postsmolts were growing isometrically with little energy storage, Fulton's *K* was unable to distinguish between fast and slow growers within the fed treatment, and *K* values of fed fish were significantly higher than those of fasted fish only on the final day of sampling (day 23). Generally, Fulton's *K* tends to have a long temporal response (weeks to months) (Busacker et al., 1990). The relations among a fish's wet weight, water weight, protein weight, and fat weight may explain this lag time. The wet weight of a fish is highly related to water weight (as was observed by Sutton et al. [2000] in Atlantic salmon parr), and water weight is much more strongly associated with protein weight than fat weight (20–40× more) (Breck, 2008). Therefore during the early stages of fasting, when fat stores are used first (Shulman and Love 1999, Jobling 2001), changes in a fish's wet weight may be fairly subtle, but once a fish begins to use protein for energy, water loss (and thus wet weight loss) would accelerate. In our study, mean fat concentration in fasted fish decreased slightly with time while mean protein concentration remained constant. Within the fasted treatment there was a decreasing trend in mean *K* values, but owing to high variability

Table 5

Pearson product-moment correlations (r) between (A) proximate body composition (g) or (B) wet-weight-based proximate body composition or instantaneous wet-weight-based growth rate of Atlantic salmon (*Salmo salar*) post-smolts, and wet weight, bioelectrical impedance analysis (BIA) measures and Fulton's K. R_{par}=resistance in parallel; Xc_{par}=reactance in parallel; D=distance between BIA detector electrodes; R_{par} and Xc_{par} *conductor volume*=D^2/R_{par} and D^2/Xc_{par}, respectively; *phase angle* (°)=arctangent of Xc/R converted to degrees; *capacitance* is a measure of the electrical storage capacity of cells; *impedance* is a measure of the opposition to the flow of electrical current; Fulton's K=(100•wet weight/fork length^3). Boldface type highlights highest correlation between body composition or growth rate, and wet weight, BIA measures, and Fulton's K. * $P \leq 0.050$, ** $P < 0.005$, *** $P < 0.0001$. n=number of fish sampled.

A

Variable	*WW*	*CP*	*TF*	*TWa*
n	69	66	61	68
Wet weight (*WW*)	1	**0.99*** **	**0.84*** **	**0.99*** **
Carcass protein content (*CP*)	0.99***	1	0.84***	0.98***
Total fat content (*TF*)	0.84***	0.74***	1	0.78***
Total water content (*TWa*)	0.99***	0.98***	0.78***	1
R_{par} conductor volume	0.92***	0.91***	0.71***	0.93***
Xc_{par} conductor volume	0.94***	0.93***	0.74***	0.95***
Phase angle	0.62***	0.60***	0.53***	0.62***
Capacitance	0.56***	0.54***	0.54***	0.54***
Impedance	−0.58***	−0.57***	−0.54***	−0.57***
Fulton's *K*	0.28*	0.31*	0.46**	0.24*

B

Variable	*WW*	*CP%*	*TF%*	*TWa%*	Growth rate
n	69	66	61	68	56
Wet weight (*WW*)	1	**0.66****	**0.48*** **	**−0.57*** **	**0.53*** **
Carcass protein concentration (*CP%*)	0.66***	1	0.32*	−0.44**	0.38*
Total fat concentration (*TF%*)	0.48***	0.32*	1	−0.93***	0.09
Total water concentration (*TWa%*)	−0.57***	−0.44**	−0.93***	1	−0.23
R_{par}/D	0.92***	0.58***	0.34*	−0.44**	0.50***
Xc_{par}/D	0.94***	0.60***	0.38**	−0.48***	0.51***
Phase angle	0.62***	0.44**	0.37**	−0.46**	0.37*
Capacitance	0.56***	0.39**	0.41**	−0.51***	0.22
Impedance	−0.58***	−0.45**	−0.41**	0.53***	−0.22
Fulton's *K*	0.28*	0.31*	0.47**	**−0.57*** **	0.32**

within a single day's sample, the values were not significantly different from day 0 (Fig. 1B). Contrary to our findings, Wilkinson et al. (2006) observed significantly lower mean K in 14-month-old Atlantic salmon smolts after 15 days of fasting (when compared to continually fed fish values), and significantly higher mean K 7 days after being refed (when compared to continually fasted fish values). By the end of our experiment (16 days after refeeding), K values for refed vs. fasted fish were not significantly different. Differences in metabolic rate or initial fat content may explain the dissimilarity in response time of K values to fasting and refeeding observed between these studies.

A significant correlation between K and total fat (r=0.74) was observed during an 18-day study of food-deprived juvenile steelhead trout (*Oncorhynchus mykiss*) (total fat range 0.4 to 3.6g) (Hanson et al., 2010). K and total fat were less correlated in our study (r=0.46) which encompassed a larger range of total fat values (1.8–12.7g). In our postsmolt Atlantic salmon, K values were not highly correlated with body composition (g or %WW) or growth rate (all $r<|0.6|$)

Estimates of conductor volume

Equations based on conductor volume have been developed to predict water-, fat- and protein-content of five species of fish (Cox and Hartman, 2005; Pothoven et al., 2008; Hanson et al., 2010). For simple cylindrical shapes, when R is measured at a constant temperature and frequency, a conductor volume (V) calculated with Ohm's law ($V=\rho L^2/R$) should approximate a physical volume (Lukaski et al., 1985). Both Cox and Hartman (2005) (brook trout) and Hanson et al. (2010) (juvenile steelhead) observed strong linear relations between conductor volume ($r^2 \geq 0.95$) and total water and protein content in their fish. The relation of total fat to conductor volume was equally high in the brook trout (r^2=0.96; Cox and

Hartman, 2005) but was not significant in the steelhead (r^2=0.02; Hanson et al., 2010). Pothoven et al. (2008) observed significant relations between conductor volume and total fat or dry mass in yellow perch (*Perca flavescens*), walleye (*Sander vitreus*), and lake whitefish (*Coregonus clupeaformis*), with r^2 values ranging from 0.62 to 0.93. In our study, we also found conductor volume to be highly correlated with carcass protein content and total water (r=0.93 and 0.95, respectively) but more weakly correlated with total fat (r=0.74). Pothoven et al. (2008) suggested that significant correlation between published conductor volumes and body composition (g) is most likely due to biases imposed by the distance between the electrodes. The consistent placement of BIA electrodes on each fish results in the numerator of the conductor volume equation becoming a proxy for the size of the fish, and fish size is highly correlated with body contents (i.e., the larger the animal, the greater its total fat, water, protein, and ash content). In both our study (protein, fat, water) and Pothoven et al. (2008; yellow perch, fat and dry weight; walleye, fat), wet weight had a stronger relation to body composition (g) than did conductor volume. Neither Cox and Hartman (2005) nor Hanson et al. (2010) reported correlation results between wet weight and body composition (g). It would be valuable to know whether wet weight could estimate total fat, protein, and water content equally well or better than BIA conductor volume in their studies as well.

Prediction models

In our study, the most parsimonious models for predicting body composition (g) all contained wet weight and fork length, and frequently a weight-length interaction term (Fulton's K). Adding any combination of the nine BIA measures to size-based-only models increased the explanatory capabilities by less than 2%. Bosworth and Wolters (2001) estimated carcass fat content in channel catfish (*Ictalurus punctatus*) using wet weight, R, and Xc as the predictor variables, resulting in an r^2=0.75. They determined that adding the BIA measures to a model containing wet weight only increased the predictive capability by 71%; however, R and Xc in their model had not been corrected for the distance between the electrodes. Because these impedance measurements are highly dependent upon the distance the current must travel between the electrodes, they must be standardized to distance when used in prediction equations (RJL Systems, http://www.rjlsystems.com/docs/bia_info/principles/, accessed April 2008) or they simply become proxies for length. Therefore the Bosworth and Wolters (2001) carcass fat content model essentially contains size-related only variables—and size is highly correlated with content values.

When body constituents are expressed as concentrations (e.g., percent wet weight), the values are less size-dependent. Pothoven et al. (2008) examined the capability of 4 models (3 of which contained BIA measures) to predict percent total fat in 3 fish species. Interestingly, all of the variables used in their models were size related (body mass, total length, conductor volume, R_{par} and Xc_{par} uncorrected for distance between electrodes). In their study, fat concentration within a species encompassed a range of values (yellow perch: 2.7–8.7%; walleye: 6.0–18.2%; lake whitefish: 2.4–14.7%), but overall predictive capability of the most parsimonious model for each species was low (r^2 range: 0.17–0.53).

In our study, all of the body composition (%WW) models also had low predictive capabilities, with less than 50% of the variability explained by any of the top 3 models. Our most parsimonious models for *TF%* and *TWa%* contained only size variables (Table 4), whereas the *CP%* and growth rate models contained both size and either 2 or 3 BIA measures (Table 4). In the *CP%* models there was little added value of BIA measures to models containing only size variables (explanatory capabilities increased by <3.4%), and in the growth-rate models, adding two BIA measures did increase the r^2 of size-based-only models by ~20%. However, the overall predictive capability of the growth-rate models was still less than 50%.

In a recent study by Hartman et al. (2011), highly predictive models for estimating percent dry weight in coastal bluefish (*Pomatomus saltatrix*) were constructed by using BIA measures. The most highly predictive models for their fish (15°C, r^2=0.86; 27°C, r^2=0.91) contained either phase angle or capacitance, plus R/D and Xc/D. Ideally, standardizing R and Xc by the distance between the electrodes (D) would eliminate the effect of size on the impedance values; however, in our study we determined that even after standardization, R_{par}/D and Xc_{par}/D were still highly correlated with size (wet weight, r>0.91, Table 5B). Correlations between size (wet weight) and candidate BIA predictor variables were not reported in the coastal bluefish study, and size (wet weight or length) was not tested as a predictor variable in any of the models.

In our study, size continually emerged as a significant variable in all of the body composition models. To our knowledge, no experiment has been conducted which controls the effect of size well enough to determine the actual contribution of BIA measures to the estimation of body composition independent of size. Until this is better understood, it will remain unclear to what extent BIA measures can improve upon size-only estimates of body composition.

Phase angle

The use of BIA-estimated phase angle as a measure of fish condition has been proposed by Cox and Heintz (2009). They concluded that in the 5 species they studied, fish with phase angles >15° were in better condition than those with phase angles <15°. Caution should be used before universally applying this 15°cut-off value. In their own study, Cox and Heintz (2009) observed 12° phase angles in field-caught Pacific herring (*Clupea pallasii*) with mass-specific energy contents of 7.15 kJ/g, and 15° phase angles in Pacific herring caught four months later with energy contents of 5.02 kJ/g. They also

reported phase angles >15° in large juvenile rainbow trout which had experienced a 9% loss of body weight after four weeks of food deprivation (Cox and Heintz, 2009). In our study, we found a low correlation (r=0.37) between growth rate and phase angle. On the basis of our results and those of Cox and Heintz (2009), we feel it is unlikely that a single phase angle value can correctly distinguish good from poor condition fish in all applications, and that the cut-off value will be influenced by factors such as life-stage, age, reproductive status, species, and temperature.

In the Cox and Heintz (2009) study, the time frame necessary to clearly differentiate fasted from fed laboratory fish by phase angle varied by species and size. Significant differences between feeding treatments were observed in small juvenile rainbow trout after 14 days of fasting, in large juvenile rainbow trout after 21 days, in juvenile brook trout after 28 days, and in juvenile Chinook salmon after >77 days. This large range of response times may reflect differences in fat reserves in the test animals. If fat reserves do affect response time, then more than just a decline in fat content would be necessary to elicit a decrease in phase angle. A decrease in protein content (with its concomitant water loss) may also be necessary for a significant decline in phase angle. If this is true, then the response time of K to food deprivation may be similar to (or possibly better than) that of phase angle. On the final sampling day of our study, K values, not phase angle, were significantly different between the fasted and fed fish. It would be interesting to know what the response time of K values were in the Cox and Heintz (2009) food-deprivation study.

Conclusions

The use of BIA as a proximate body composition estimator or fish condition index is relatively new. As with any condition index, its validity must be established for the specific application in which it will be used. Field personnel are seeking a nonlethal index that can reflect the condition of Atlantic salmon postsmolts 2 to 3 weeks after the fish are released from the hatchery, when the majority of postsmolts are captured on targeted trawl surveys. We designed an experiment to evaluate the utility of BIA and Fulton's condition factor as indices of condition during that time-frame. Results of our study indicated that 1) growth rates of postsmolts responded rapidly to the withholding and re-introduction of food; 2) fed postsmolts grew isometrically; and 3) 3 weeks of withholding food is not sufficient time to elicit significant declines in proximate body constituents in fasting postsmolts. This combination of isometric growth in fed fish and short-term starvation period in fasting fish resulted in nonsignificant differences in body composition (%WW) among the feeding treatments (fed; fasted; fasted, then refed). The utility of BIA and Fulton's K as condition indices depends upon detecting differences in proportions of body constituents. During our study, BIA measures were not significantly different among the 3 feeding treatments, and only on the final day of sampling was K in fasted fish significantly less than in fed fish. Our study has demonstrated that neither BIA nor Fulton's K would be an appropriate choice of index 1) to reflect short-term changes (weeks rather than months) in postsmolt condition, or 2) to monitor fish condition during a life-stage where excess energy is primarily directed toward isometric growth rather than energy storage. We propose that a methodology that measures growth rate (directly or indirectly) would be a more suitable condition index for isometric growth life-stages. We will be reporting on the utility of two potential growth-rate indices in Atlantic salmon postsmolts in a later publication.

Results from our study also supported conclusions by Pothoven et al. (2008) that simple measures of size were better predictors of body composition than BIA measures. Additionally, we observed that Fulton's K responded more quickly to food deprivation than BIA measures, and that a single cut-off value for phase angle, as a distinction between good and poor condition fish, should be used with caution. BIA is an emerging technique in fishery biology, and as such, its application will require more research to identify its appropriate use.

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Estimation of discard mortality of sablefish (*Anoplopoma fimbria*) in Alaska longline fisheries

Megan M. Stachura[1,2]
Chris R. Lunsford (contact author)[1]
Cara J. Rodgveller[1]
Jonathan Heifetz[1]

Email address for contact author: chris.lunsford@noaa.gov

[1] Auke Bay Laboratories
Ted Stevens Marine Research Institute
Alaska Fisheries Science Center
National Marine Fisheries Service
National Oceanic and Atmospheric Administration
17109 Pt. Lena Loop Rd.
Juneau, Alaska 99801

[2] Present address:
School of Aquatic and Fishery Sciences
University of Washington
Box 355020
Seattle, Washington 98195

Abstract—Sablefish (*Anoplopoma fimbria*) are often caught incidentally in longline fisheries and discarded, but the extent of mortality after release is unknown, which creates uncertainty for estimates of total mortality. We analyzed data from 10,427 fish that were tagged in research surveys and recovered in surveys and commercial fisheries up to 19 years later and found a decrease in recapture rates for fish originally captured at shallower depths (210–319 m) during the study, sustaining severe hooking injuries, and sustaining amphipod predation injuries. The overall estimated discard mortality rate was 11.71%. This estimate is based on an assumed survival rate of 96.5% for fish with minor hooking injuries and the observed recapture rates for sablefish at each level of severity of hook injury. This estimate may be lower than what actually occurs in commercial fisheries because fish are likely not handled as carefully as those in our study. Comparing our results with data on the relative occurrence of the severity of hooking injuries in longline fisheries may lead to more accurate accounting of total mortality attributable to fishing and to improved management of this species.

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For stock assessment, accurate accounting of discard mortality is important for estimating total mortality attributable to fishing. Studies of sablefish (*Anoplopoma fimbria*) and other fish species show that catch-related injuries can cause delayed mortality after a fish is discarded. For example, sablefish laboratory experiments have shown that the level of physical injury, reflex impairment, and behavior impairment may be useful proxies for delayed mortality (Davis, 2005; Davis and Ottmar, 2006). Pacific halibut (*Hippoglossus stenolepis*) with more severe hook injuries had increased mortality and reduced growth compared to those with less severe injuries (Kaimmer, 1994; Kaimmer and Trumble, 1998) and were visually impaired after exposure to simulated sunlight (Brill et al., 2008). For Atlantic cod (*Gadus morhua* L), injuries to the eyes, gills, and belly were more lethal than injuries to other anatomical parts (Pálsson et al., 2003). After release, Atlantic cod had inhibited activity for 4 days, during which there was potentially increased susceptibility to predation and delayed mortality (Neat et al., 2009).

A first step in estimating discard mortality is to estimate the proportion of fish that die after being discarded. Estimates of sablefish discard mortality rates and the derivation methods for determining these estimates vary regionally and by management agency. In the southeast Alaska sablefish stock assessment conducted by the Alaska Department of Fish and Game for state waters, a 25% discard mortality rate in the Pacific halibut longline fishery is assumed for sablefish (Dressel[1]). For both trawl and longline federal groundfish fisheries in Alaska, 100% mortality is assumed for all sablefish that are discarded (Hanselman et al., 2010). In the federal Pacific Coast sablefish stock assessment a much lower discard mortality rate of 10% is assumed for longline gear (Schirripa, 2008).

Sablefish support one of the most valuable fisheries in Alaska (Hiatt et al., 2010). The fixed gear fishery in

[1] Dressel, S. C. 2009. 2006 northern southeast inside sablefish stock assessment and 2007 forecast and quota. Fishery Data Series 09-50, 78 p. Alaska Dep. Fish Game, Anchorage, AK.

federal waters off Alaska is managed by a catch shares program, where annual individual fishing quota (IFQ) shares are allocated to fishermen, for fish that can be caught anytime during the eight and a half month season. For fishermen with IFQs, full retention of all sablefish caught is required. However, sablefish are often legally discarded in other commercial longline fisheries, primarily in those targeting Pacific halibut and Pacific cod (*Gadus macrocephalus*). In the sablefish fishery, the practice of releasing small sablefish and retaining only the larger fish because of the greater value per pound of larger fish (a technique known as "highgrading" [Davis, 2002]) is illegal. However, because there is an incentive to retain larger fish and not all fishing trips are monitored, highgrading may occur.

Factors affecting discard mortality likely vary by species, gear type, depth, and other environmental factors. Injury location on fish has proven to be an indicator of short and long-term discard mortality (e.g., Bartholomew and Bohnsack, 2005). In Alaska, sablefish inhabit a wide range of depths and are caught primarily on longline gear, which can cause external injuries to different areas of the body. Fish tethered to longline gear for extended periods are subject to predation by parasitic amphipod crustaceans. Also fish size may affect mortality of discarded fish. The objective of our study is to determine if the location and severity of the hook injury, line and roller gear injury, water depth, fish size, and the level of amphipod predation affect the discard mortality rate in Alaskan longline fisheries. To answer these questions, the recapture rates of fish tagged and released in the marine environment were related to each factor. In addition, an absolute discard mortality rate was computed on the basis of the observed severity of hooking injuries.

Materials and methods

Tagging and data collection

In 1989 and 1990, research surveys were conducted by the National Marine Fisheries Service (NMFS), Alaska Fisheries Science Center (AFSC) in Southeast Alaska. In 1989, sablefish were tagged during August and September in Chatham Strait; in 1990, sablefish were tagged during April and May in Clarence Strait (Fig. 1). Longline gear was fished on the bottom at depths from 210 to 419 m with a minimum 3-hour soak time. Gear configuration consisted of size 13/0 circle hooks baited with squid attached to 38-cm gangions that were secured to beckets tied in a 9.5-mm (3/8 in) groundline at 2-m intervals. This gear configuration is similar to that used in the commercial sablefish fishery in Alaska. However, the Pacific halibut fishery typically uses larger hooks (16/0). All sablefish, except those with extremely severe injuries, were tagged with plastic T-bar style anchor tags, and injuries were classified by the following 4 variables: location of hook injury, severity of hook injury, severity of injuries due to amphipod predation, and the presence of injury sustained on fins or body from line and roller gears. Within each variable, a categorical condition code describing the injury was recorded (Table 1). The date of capture, capture location, and depth of capture were also documented. Fish were promptly released after they were measured (fork length, nearest mm) and tagged.

To determine recapture rates of fish within each category, tagged fish were recovered in commercial fisheries and tags were returned to the AFSC for a reward (Maloney[2]). Tags were also recovered during subsequent research studies. Data for fish recaptured from the time of tagging to June 2009 were used in our analysis (up to 19 years at liberty).

Analysis

A logistic regression model was constructed to determine which factors were related to significant differences in recapture rates. The relationship between the binary, dependent variable, Y_i, which represents whether a fish was recaptured or not, and seven independent explanatory variables was estimated with the following full model,

$$Logit(Y_i) = a + bYr_i + cL_i + dD_i + eHL_i + fHS_i + gA_i + hG_i, \quad (1)$$

where a = the intercept, and b to h are estimated model coefficients;
Yr_i = year of tagging (1989, 1990);
L_i = fish length at capture;
D_i = capture depth group (210–269, 270–319, 320–419 m);
HL_i = location of the hook injury (cheek, upper jaw, lower jaw, nose, throat, eye, gill);
HS_i = severity of the hook injury (minor, moderate, severe);
A_i = severity of amphipod predation injury (no injury, ≤10% scale loss, >10% scale loss); and
G_i = type of injury sustained on fins or body from line and roller gears (no injury, fin damage, lacerations) for fish i (Table 1).

Year can also be considered to be the effect of location because in each year fish were tagged at different locations. All independent variables were treated as categorical except for length, which was continuous. Interaction terms were not included in the model because of the small sample sizes available across multiple categorical variables, which resulted in an inability to estimate these interaction parameters.

Forward-stepwise model selection was performed to simplify the model to factors that significantly improved

[2] Maloney, N. E. 2002. Report to industry on the Alaska sablefish tag program, 1972–2001. AFSC Processed Rep. 2002-01, 44 p. Auke Bay Laboratory, NMFS, NOAA, 11305 Glacier Highway, Juneau, AK 99801.

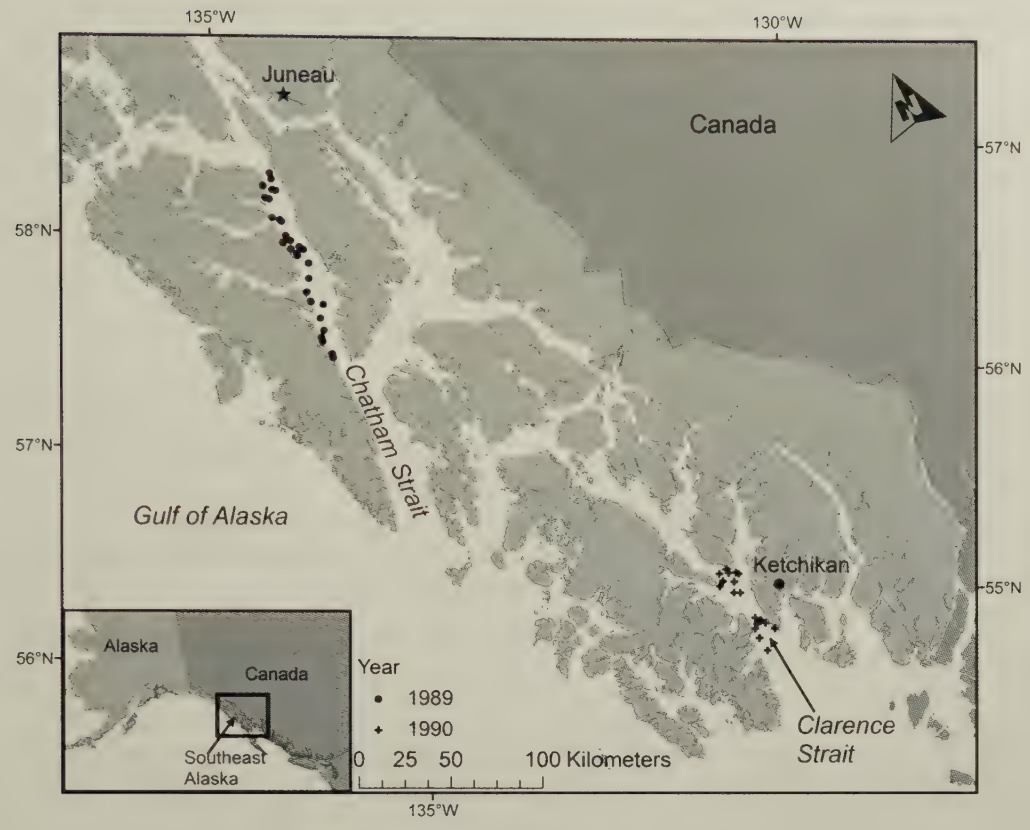

Figure 1

Map of the areas in Southeast Alaska where sablefish (*Anoplopoma fimbria*) were tagged during research surveys in 1989 (•) and 1990 (+).

model fit. The model with the minimum Akaike information criteria (AIC) value was chosen. A Wald chi-squared test was used to calculate the overall significance of categorical variables with multiple coefficients. All statistical analysis was implemented in R software, vers. 2.11.1 (R Development Core Team, 2010) including use of the aod package, vers. 1.2 (Lsenoff and Lancelot, 2010).

Recapture rates for categories within each variable were calculated by dividing the number of recaptured fish by the number of tagged fish for each category. Absolute survival rates were calculated for each level of hook severity on the basis of observed recapture rates and the survival rate of a Pacific halibut with minor hooking injuries (Kaimmer, 1994; Kaimmer and Trumble, 1998; Trumble et. al., 2000). Previous studies have determined that the expected survival of a properly handled Pacific halibut is in the 95–98% range; a released fish with minor injuries has an estimated 96.5% survival rate (Trumble et al., 2000). We used the Pacific halibut estimate of survival rate as a proxy for that of sablefish for the following reasons: these species do not experience barotrauma as a result of rapid decompression; they co-occur in the same water temperatures, areas, and depths; they are caught with nearly identical gear types; and they are commonly fished by the same fishing vessels and crew. Like Pacific halibut, sablefish are hardy and, when handled appropriately, have high survival rates after capture and discard. Long-term tagging programs for both species provide evidence of their hardiness (Kaimmer, 2000; Maloney[2]). The hardiness of sablefish is also supported by previous research in a laboratory setting where there was 100% survival after 60 days (Davis et al., 2001). Ours is the first dedicated study to estimate sablefish discard mortality. Previous estimates of Pacific halibut survival rates are the best available data to use as a proxy for sablefish.

The average survival rate of fish with different severities of hook injury, i.e., the absolute survival rate, was estimated on the basis of recapture rates and relative frequency of all 3 levels of hook injury (minor, moderate, severe) by using the methods in Kaimmer and Trumble (1998). The overall absolute survival rate (S) of captured fish was calculated with the following formula:

$$S = \frac{\left(\frac{R_0 + R_1 + R_2}{T_0 + T_1 + T_2 + NT}\right)}{\frac{R_0}{T_0}} \times 0.965, \quad (2)$$

where T_0, T_1, and T_2 and R_0, R_1, and R_2 are the number of fish tagged (T) and recovered (R) with minor (0), moderate (1) and severe hook injuries (2). Fish that were not

Table 1

Description and assigned injury code for injury types and severities for sablefish (*Anoplopoma fimbria*) caught on longline gear, for an estimation of discard mortality.

Factor	Description
Hook injury location	
0	Hooked in cheek or parts of operculum
1	Hooked in upper jaw: maxilla or premaxilla
2	Hooked in lower jaw: dentary (mandible)
3	Hooked in nose or snout
4	Hooked in throat
5	Hooked in eye
6	Hooked around gill or gill arches
Hook injury severity	
0	Minor: small puncture, flesh not torn, no abrasion
1	Moderate: flesh torn; some abrasion; bones intact, eye orbit not punctured
2	Severe: bones torn at insertion, severed or shattered, gills hooked but no broken gill arches, hooked through palatine into nose capsule, cheek bones shattered, hooked in throat and bleeding but not torn
NT	No tag: gill arches torn or bleeding, hook swallowed with substantial tears in throat; maxillary and premaxillary or dentary torn off; nose or snout smashed
Amphipod predation injury	
0	No injury
1	Moderate scale loss: 10% or less
2	Heavy scale loss: greater than 10%
Line and roller gear injury sustained on fins or body	
0	No injury
1	Fin damage: caudal, pectoral, pelvic, dorsal, or anal fin
2	Lacerations: line markings across body

tagged because of the extreme severity of their injuries were assumed to have 0% survival and are represented in the equation as *NT* (having no tag and they were included in the total number of fish caught when calculating the recovery rate for each injury group). The survival rate of fish in each category was calculated with the following formula:

$$S_x = \frac{\left(\frac{R_x}{T_x}\right)}{\frac{R_0}{T_0}} \times 0.965, \quad (3)$$

where all variables are the same as in Equation 2 and x represents the severity of the hook injury (0, 1, or 2).

Results

A large number of sablefish were captured (10,940) and tagged (10,508): 8838 fish were tagged during the 1989 survey and 1670 during the 1990 survey. A substantial number of fish were recaptured (1207 fish, 11.49% recapture rate of tagged fish) between 9 days and 19.2 years (mean=3.4 yr, standard deviation=4.5 yr) after tagging. Because some data were lacking for 81 fish, analyses were run with data from 10,427 fish. An additional 432 fish were captured but not tagged because of the extreme injuries from capture or amphipod predation (*NT* in Eq. 2, see *Materials and methods* section).

Logistic regression model

The reduced model was chosen on the basis of the smallest AIC value. Several parameters were found to significantly affect recapture rates: year (which also can be considered to be a location effect), depth, severity of hook injury, and amphipod predation (Table 2, Fig. 2). Fish tagged in 1989 had a lower recapture rate (11.26%) than those tagged in 1990 (12.66%) (Table 3). Fish from the greatest depths (320–419 m) had a greater rate of recapture (14.33%) than fish captured at shallower depths (210–269 m, 10.61%; 270–319 m, 10.43%; Table 3). Severity of hook injury also exhibited a significant effect on the recapture of tagged fish (Table 2). Fish with severe injuries had a lower recapture rate (8.49%) than those with minor (12.05%) or moderate (11.81%) injuries (Table 3). The confidence intervals surrounding the parameters for severity of injury were relatively narrow, with the 95% confidence interval of the odds

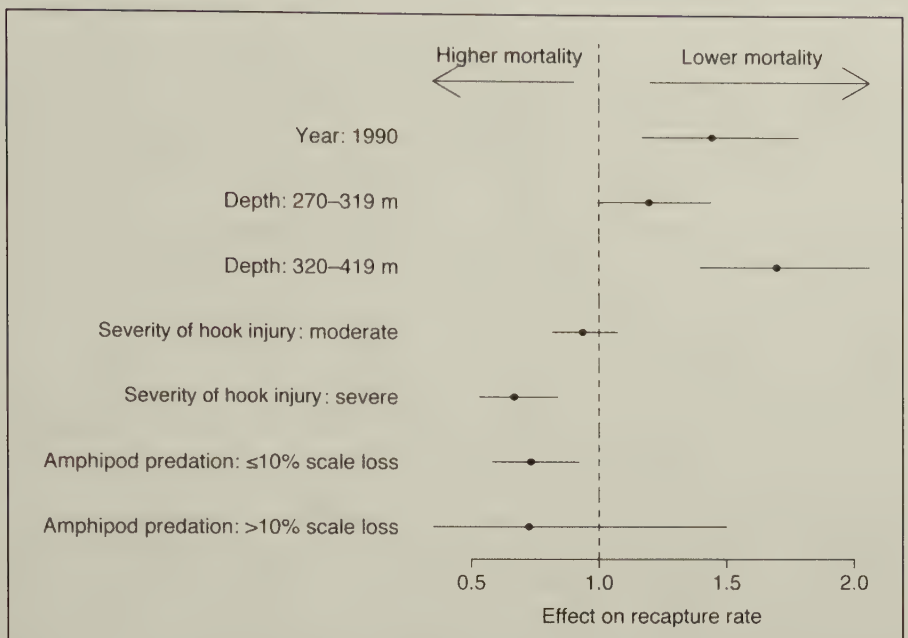

Figure 2

Comparison of the effects of the variables in the final model on the recapture rate of tagged sablefish (*Anoplopoma fimbria*). The effect on recapture (circle) is the exponent of the estimated parameter for the variable in the logistic regression and is the odds ratio: the odds of recapture of a fish in a category compared to the odds of recapture in the initial category of the categorical variable (year: 1989; depth: 210–269 m; severity of hook injury: minor; amphipod predation: no predation). Horizontal lines are 95% confidence intervals for the estimate.

ratio for the effect of severe hooking injuries <1, indicating a significant negative effect on recapture (Fig. 2). Although only a small portion of the fish sampled suffered from amphipod predation, it significantly affected recapture and was included in the final model (Table 2). Fish with no observed amphipod predation had a higher rate of recapture (11.86%) than fish with ≤10% scale loss (8.44%) and fish with >10% scale loss (7.84%) owing to amphipod predation (Table 3). The 95% confidence interval of the odds ratio for the effect of less than or equal to 10% scale loss was less than 1, indicating a significant negative effect on recapture (Fig. 2). However, there was a high amount of variability around the estimated parameter for the effect of >10% scale loss because of a low number of samples (Fig. 2). The majority of fish (51.06%) that were too severely injured to be tagged had suffered from amphipod predation, and only 11.09% of fish that were healthy enough to be tagged had suffered amphipod predation.

In our study location of hook injury, fish length, and type of gear injury did not significantly affect recapture rates. Hook injuries were not in critical locations that would likely cause mortality alone. Most injuries were located on the cheek and upper and lower jaws (95.53%). There were a small number of fish observed that had hook injuries to other areas of the body (nose, throat, eye, gill; 4.47%) (Table 3). A wide range of fish lengths were included in our study, but length did not have a significant effect on recapture rate. Injuries caused by the line and roller gear also did not have a significant effect on recapture rate. This result may be the consequence of low statistical power because few fish (5.58%) sustained injuries caused by gear other than hooks (Table 3).

Table 2

Significant effects included in the reduced logistic regression model, where the response is whether a sablefish (*Anoplopoma fimbria*) was successfully recaptured after tagging. The overall variable significance was calculated by using a Wald chi-squared test.

Variable	χ^2	df	$P(>\chi^2)$
Intercept	571.0	1	<0.001
Year	11.6	1	<0.001
Depth (m)	34.8	2	<0.001
Severity of hook injury	12.4	2	0.002
Amphipod predation	7.7	2	0.021

Survival rates

The absolute survival rate of fish in each category of severity of hook injury was calculated with Equation 3

Table 3

Number of sablefish (*Anoplopoma fimbria*) tagged and recaptured (number and %) by each variable. Length was a continuous variable in the analysis but is categorized here for summary purposes. The estimated absolute survival was estimated for the levels of the severity of hook injury on the basis of an assumed 96.5% survival of fish with minor injuries.

Variable	Tagged	Recaptured	% Recaptured	Estimated absolute survival %
Year				
1989	8768	987	11.26	
1990	1659	210	12.66	
Length (cm)				
<60	1280	152	11.88	
60–69	5250	585	11.14	
70–79	3048	360	11.81	
>80	849	100	11.78	
Depth (m)				
210–269	3354	356	10.61	
270–319	4428	462	10.43	
320–419	2645	379	14.33	
Hook location				
Cheek	3290	396	12.04	
Upper jaw	1759	199	11.31	
Lower jaw	4912	559	11.38	
Nose	123	14	11.38	
Throat	212	17	8.02	
Eye	120	11	9.17	
Gill	11	1	9.09	
Severity of hook injury				
Minor	2963	357	12.05	96.50
Moderate	6204	733	11.81	94.63
Severe	1260	107	8.49	68.01
Extreme	432			0.0
Total	10,859	1197	11.02	88.29
Amphipod predation				
No predation	9271	1100	11.86	
≤10% scale loss	1054	89	8.44	
>10% scale loss	102	8	7.84	
Gear injury				
No injury	9845	1133	11.51	
Fin damage	539	57	10.58	
Lacerations	43	7	16.28	

(Table 3). The overall absolute survival of released sablefish was estimated, with Equation 2, to be 88.29%, or an overall mortality rate of 11.71% (Table 3). The absolute survival of fish with severe injuries (68.01%) was much lower.

Discussion

Our results indicate that the severity of hook injury is related to recapture rates for tagged sablefish. Most injuries were to the cheek and jaw and not to critical areas, such as the gills and brain. The severe injuries that we saw likely resulted in delayed mortality following the tagging event which would explain lower recapture rates. The severity of an injury is likely influenced by the technique for hook removal. Previous studies with Pacific halibut (Kaimmer, 1994; Kaimmer and Trumble, 1998) found that the removal of the hook affects the severity of the hook injury and, as with sablefish, survival decreased with an increase in the severity of hook injury. Severity of hook injury is a logical parameter for estimation of discard mortality because it significantly affects recapture rate.

In our study, the location of hooking injury did not significantly affect recapture rates. However, a large portion of injuries occurred on the cheek and upper and lower jaws—locations that are typically affected by circle hooks. We likely did not have enough samples of fish with injuries in other locations to detect the effects of those injuries. Unlike our results, results from studies of catch-and-release of recreationally caught species have indicated that hooking location was the most significant factor in estimating mortality (reviewed in Bartholomew and Bohnsack, 2005). Deep-hooking injuries in critical locations such as the esophagus, stomach, gills, eyes, and brain significantly increase mortality in many species (e.g., Muoneke and Childress, 1994; Pálsson et al., 2003; Aalbers et al., 2004; Alós et al., 2009). The circle hooks that are used in Alaska longline fisheries usually hook fish in the mouth and injuries in critical locations are not common (reviewed in Trumble et al., 2000). Capture with other hook types or fishing gears, such as trawl gear, would likely produce injuries on other locations of the body.

Depth of capture significantly affected the recapture rate of sablefish, which is common for other fish species. We found a positive relationship between depth of capture and assumed survival (i.e., fish caught at shallow depths were less likely to be recaptured). The sablefish fishery extends to at least 800 m in many areas and so the effect of depth on recapture rates may be even more pronounced at depths greater than 419 m, the maximum sampling depth in our study. The opposite has been observed in physoclistous species due to barotrauma, because of organ damage caused by gas expansion in the body cavity during capture (e.g., Gitschlag and Renaud, 1994; Wilson and Burns, 1996; Collins et al., 1999; St. John and Syers, 2005). Sablefish lack a swim bladder, thus no correlation between mortality and depth of capture was expected. Deeper-dwelling fish can also have increased injuries with greater capture depths, indicating that injuries are inflicted while fish struggle during hauling (Atlantic cod; Pálsson et al., 2003).

There are some potential explanations for why fish caught at shallow depths had lower recapture rates. First, sablefish caught at deeper depths (320–419 m) could be less vigorous because of the longer retrieval time and the increased time spent fighting the line during retrieval and therefore they are less likely to become injured during the landing process when out of the water and onboard the fishing vessel. Differential predation in the depth categories may also affect the mortality of released sablefish, if they return to their previous depths after release. Two major predators of sablefish have greater concentration at shallower depths, Pacific halibut (27–274 m; IPHC, 1998) and Pacific sleeper sharks (*Somniosus pacificus*) (Yano et al., 2007). Second, fishing effort likely differs by depth and therefore may affect depth-related recapture rates of tagged fish. Data on fishing effort by depth were not available from the Pacific halibut fishery or the southeast Alaska state sablefish fishery and therefore a full examination of this supposition was not possible.

In our study, amphipod predation was related to the recapture rate of sablefish and was prevalent for fish that were too severely injured to tag. Similarly, Pacific halibut that were tethered to longlines for extended periods suffered from amphipod predation and had a low survival rate (Trumble et al., 2000). Fishery-specific amphipod predation rates would need to be investigated to accurately assess this effect on the discard mortality of sablefish.

The year of capture significantly affected the recapture rate of sablefish. A greater recapture rate was found for fish tagged in Clarence Strait in 1990 and several factors likely contributed to this difference. First, a greater proportion of fish tagged in 1990 (18.57%) were recaptured within 60 days of tagging compared to those tagged in 1989 (7.42%). This is likely explained by the occurrence of an Alaska Department of Fish and Game sablefish survey and the southern southeast Alaska directed sablefish fishery both occurring within 60 days of the initial tagging effort. Tagging conducted in Chatham Strait in 1989 occurred after both the state survey and fishery period and therefore the grounds were not fished for nearly a year after the tagging effort. A minimum time at liberty was not used in our study because the year or location of tagging was secondary to our primary objective of determining the factors related to discard mortality and estimating absolute discard mortality based on the severity of injuries to sablefish. Second, longline fishing is permitted in the Chatham Strait fishery, and in Clarence Strait both longline and pot gear are allowed. Animals can exhibit varying levels of "trap addiction" (attraction to fishing gear) or "trap shyness" (an aversion to the gear) depending on the gear type (Seber, 1982). Previous tagging analyses have shown that sablefish may be trap shy towards longline gear within the first year after capture, likely because of the stress incurred during the initial capture (Carlile, et al.[3]). Because many of our fish were caught soon after capture in the fishery, some of the difference in recapture rate that we saw may be explained by the differential recapture catch rates between pot and longline gear types. Finally, amphipod predation was significantly higher in 1989 (12.45%) than in 1990 (3.86%) indicating that Chatham Strait may have a higher incidence of amphipods, which we found to be related to a decreased recapture rate.

We calculated an absolute mortality rate for each level of severity of hook injury. The overall mortality rate of 11.71% is substantially lower than the 25% mortality rate assumed for sablefish discarded in the Pacific halibut fishery in state waters (i.e., Chatham

[3] Carlile, D., B. Richardson, M. Cartwright, and V. M. O'Connell. 2002. Southeast Alaska sablefish stock assessment activities 1998–2001. Regional Information Report IJ02-02, 86 p. Alaska Dep. Fish and Game, Douglas, AK.

and Clarence Straits; Dressel[1]), and the assumed 100% mortality of sablefish caught in other target fisheries in federal waters in Alaska (Hanselman et al., 2010). Applying the 11.71% mortality rate to the average catch of sablefish discarded in federally managed hook-and-line fisheries (491 t, 2004–09 average; Hanselman et al., 2010), yields an annual discard mortality of 57.5 tons.

There are two reasons why our estimate of absolute discard mortality may be lower than what occurs in the commercial fishery. First, in our study fish were handled carefully and released, whereas in commercial fisheries we would expect a greater proportion of moderate and severe injuries that would result in a higher discard mortality. Second, commercial fishery discards come from multiple fisheries that use numerous gear types, most notably different hook types and sizes. Larger hooks have been shown to result in higher discard mortality (Trumble et al., 2000). Because the halibut fishery in Alaska uses larger hooks than we used in our study, a higher discard mortality rate for sablefish would be expected in the halibut fishery. Careful hook removal during release of fish could potentially minimize discard mortality rates observed in commercial fisheries.

Conclusion

In this study we examined some of the factors that affect the discard mortality rate of sablefish in Alaskan longline fisheries. We found a decrease in recapture rates for fish originally captured at shallower depths (210–319 m) in our study, sustaining severe hooking injuries, and sustaining amphipod predation injuries. Based on the severity of hook injury, we estimated an overall discard mortality rate of 11.71%. Obtaining data on the relative occurrence of the severity of hook injuries that occur in these fisheries is a logical next step. Such data would allow us to extrapolate our findings more reliably and may lead to a more accurate accounting of total mortality attributable to fishing and to improved management of this species.

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